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Evolutionary Relationships, Osteology, and Zoogeography of Leptodactyloid Frogs

By

John D. Lynch

UNIVERSITY OF KANSAS
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June 30, 1971

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University of Kansas
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By

John D. Lynch
Department of Zoology
University of Nebraska
Lincoln, Nebraska 68508

University of Kansas
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INTRODUCTION

Frogs of the family Leptodactylidae *(auctorum)* are distributed throughout the Neotropics north to Texas and Florida, in southern Africa, and over most of the Australo-Papuan region (Fig. 1). The family is one of the largest amphibian families and was known to the early describers of the world's fauna. Linné (1758) knew two species of the family, *Rana ocellata (=Leptodactylus ocellatus)* and *Rana cornuta (=Ceratophrys cornuta),* and the tadpole of a third, *Lacerta caudiverbera (=Caudiverbera caudiverbera),* all from South America. The first representative of the Australian fauna was not described until Shaw's (1795) work naming *Rana australiaca (=Heleioporus australiacus).* The family, as presently conceived, contains approximately 650 species in 57 living genera arranged in seven subfamilies. Two of these subfamilies are restricted to Australia, New Guinea, and Tasmania, one to the Cape region of southern Africa, and the other four to the Neotropics. Seventeen genera are restricted to the Australo-Papuan realm, one to south Africa, and 39 to the Neotropics.

Three factors have contributed to our current deplorable lack of general knowledge concerning this large family: 1) the most recent synopsis of a revisionary nature is that of Boulenger, 1882; 2) the bewildering number of generic names and the indiscriminant application of family and subfamily names of numerous authors; and 3) the problem of dealing with *Eleutherodactylus,* one of the largest vertebrate genera known. No part of this genus (either systematic or geographic) has been monographed.

Initially, this study was restricted to a survey of the skeletal morphology of frogs of the genus *Eleutherodactylus;* however, this proved impractical, because of the lack of understanding of

FIGURE 1. Distributions of the family Leptodactylidae (stipple) and the pelobatid subfamily Megophryinae (hatching).

intrageneric relationships. Therefore, I decided to re-evaluate the genera of the family and to attempt to point out suprageneric relationships. Detailed study and analysis of infrageneric relationships have, of necessity, been postponed, pending a more complete and realistic understanding of the genera involved.

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NOMENCLATORIAL RESUMÉ

More genera are contained in the Leptodactylidae than in any other amphibian family. The most recent author to monograph the Leptodactylidae was Boulenger (1882), whose analysis suffered from a misunderstanding of what characters were of use in assessing families (Noble 1922, 1931). Boulenger (1882) recognized 179 species of leptodactylids and placed them in 34 genera in 7 families. No author subsequent to Boulenger has treated any major section of the Neotropical leptodactylid fauna, other than Parker (1927), who treated the frogs then placed in *Paludicola* [=*Physalaemus*, *Pleurodema*, and *Pseudopaludicola*], although several works of major importance have appeared treating faunal units and therefore parts of leptodactylid genera (Cei, 1962a; Cochran, 1955; and Cochran and Goin, 1970).

Gallardo (1965) presented a "synopsis of leptodactylids in South America" but this work in my opinion falls far short of its intended goal. Parker (1940) and Moore (1961) provided a good understanding, albeit incomplete, of the Australo-Papuan leptodactylids. The status of the species of *Heleophryne* in South Africa is now relatively well known.

Twenty-three family group names have been proposed for frogs based on type-genera which are here included in the Leptodactylidae (Table 1). A number of other family group names have been applied to leptodactylid frogs but do not have nomenclatural significance in a classification of the leptodactylids.

Tschudi (1838) proposed two family group names, Cystignathi and Ceratophrydes, based on *Cystignathus* Wagler, 1830, and *Ceratophrys* Wied, 1824, respectively. Although the Cystignathi was widely used (Cystignathidae of Boulenger, 1882; Nieden, 1923), few authors (Cope, 1866 and Miranda-Ribeiro, 1926) used the Ceratophrydes (or an emendation of it). The concept of the group changed whenever it was used. Parker (1935) pointed out that Noble's (1931) Pseudinae was probably an artificial assemblage and regardless should take the oldest available name, Ceratophryinae. Recently, several authors have proposed using Ceratophryidae (or an emendation of this name) as a family containing three genera of Neotropical frogs. With the discovery that *Cystignathus* was an obligate synonym

TABLE 1. Family group names proposed in the Leptodactylidae and the subfamilial or tribal name used herein.

Name proposed	Name used herein
Cystignathi Tschudi, 1838	Leptodactylinae
Ceratophrydes Tschudi, 1838	Ceratophryinae
Telmatobii Fitzinger, 1843	Telmatobiinae, Telmatobiini
Myobatrachidae Schlegel, 1850	Myobatrachinae
Uperoliidae Günther, 1859	Myobatrachinae
Hylodidae Günther, 1859	Eleutherodactylini
Criniae Cope, 1866	Myobatrachinae
Pleurodemae Cope, 1866	Leptodachtylinae
Alsodina Mivart, 1869	Alsodini
Cacotina Mivart, 1869	Alsodini
Paludicolina Mivart, 1869	Leptodactylinae
Plectromantidae Mivart, 1869	Leptodactylinae
Grypiscina Mivart, 1869	Grypiscini
Leptodactylidae Berg, 1896 (1838)[a]	Leptodactylinae
Elosiidae Miranda-Ribeiro, 1926	Elosiinae
Heleophryninae Noble, 1931	Heleophryninae
Cycloraninae Parker, 1940	Cycloraninae, Cycloranini
Telmatobiinae Vellard, 1951	[Homonym]
Cyclorhamphinae Lutz, 1954	Grypiscini
Eleutherodactylinae Lutz, 1954	Eleutherodactylini
Calyptocephalellinae Reig, 1960	Telmatobiini
Batrachylinae Gallardo, 1965	Alsodini
Pseudopaludicolinae Gallardo, 1965	Leptodactylinae
Limnodynastini	Proposed herein
Odontophrynini	Proposed herein

[a] The family name Leptodactylidae is a conserved name in the sense of Article 40 (International Code of Zoological Nomenclature, 1961) and hence dates from 1838, not 1896, for purposes of priority.

of *Leptodactylus* Fitzinger, 1843, the family group name Cystignathidae became unavailable according to the rules then in effect, and Leptodactylidae was proposed as a family replacement name —this name has gained nearly universal acceptance and is thus a conserved name in the sense of the provisions of Article 40 of the International Code of Zoological Nomenclature (1961) and takes priority over any other names proposed between 1838 and 1896. Therefore the oldest valid family group name for these frogs is Berg's (1896) Leptodactylidae. Tschudi (1838) knew eleven genera and twelve species of frogs that are now placed in the Leptodactylidae. He arranged them in five families—Bombinatores *(Pleurodema* and *Telmatobius),* Ceratophrydes *(Ceratophrys* and *Phrynoceros),* Cystignathi *(Cystignathus* and *Crinia),* Hylae *(Cornufer, Elosia,* and two species of *Hylodes),* and Ranae *(Cycloramphus* and *Peltocephalus).*

Fitzinger, an active and often erratic classifier, proposed (1843) placing the 25 genera known to him in 7 families—Alytae *(Calyptocephalus, Ceratophrys, Crinia, Hammatodactylus, Leiuperus, Phrynoceros, Stombus,* and *Tomopterna),* Gastrophrynae *(Paludicola),* Limnodytae *(Eulıyas, Hylodes,* and *Lithodytes),* Pelobii *(Enydrobius),* Phyllobatae [an older family name for Dendrobatidae *(Crossodactylus* and *Scinacodes)*], Ranae *(Cystignathus, Cycloramphus, Eupsophus, Gnathophysa, Leptodactylus, Limnodynastes, Limnomedusa, Physalaemus,* and *Sibilatrix).* Burger (1954) correctly pointed out that the terminal endings of family group names such as these proposed by Fitzinger do not affect their priority and that Vellard's (1951) Telmatobiinae is a homonym of Fitzinger's Telmatobii.

Günther (1859a) attempted a worldwide catalogue of the amphibians, and, although less successful than Boulenger's (1882) second edition of this important project of the British Museum, it did present a synthesis of most of the genera of frogs as then known. Günther's family concepts were very different from those used during the following century, which explains in part why he placed the 23 leptodactylid genera known to him in eleven families—Alytidae *(Heleioporus),* Brachycephalidae *(Pseudophryne),* Bombinatoridae *(Alsodes* and *Telmatobius),* Cystignathidae *(Cystignathus, Leiuperus, Limnodynastes,* and *Pleurodema),* Discoglossidae *(Chiroleptes),* Engystomatidae *(Chelydobatrachus),* Hylodidae *(Crossodactylus* and *Hylodes),* Myobatrachidae *(Myobatrachus),* Polypedatidae *(Cornufer* and *Elosia),* Ranidae *(Calyptocephalus, Ceratophrys, Cyclorhamphus, Hylorhina, Limnocharis, Pithecopsis,* and *Pyxicephalus),* and Uperoliidae *(Uperoleia).* Of these eleven families, the Hylodidae and Uperoliidae represented new groups based on leptodactylid genera. The Hylodidae was based on *Hylodes* of Fitzinger (1843, not 1826), and thus applies to the group I designate as Eleutherodactylini; in addition, the type genus, *Hylodes* Fitzinger (1843), is a homonym. Myobatrachidae was first used by Schlegel (1850). It perhaps reflects the difficulties of communication that Günther recognized both *Chelydobatrachus* and *Myobatrachus,* which are synonymous, and included them in different families, Engystomatidae and Myobatrachidae.

Cope (1866) considerably altered the previous classifications, and relied so heavily on osteological characters that most subsequent authors have overreacted (in my opinion) in arguing that the osteocranium cannot reasonably serve in anuran classification. Cope recognized 37 genera of leptodactylid frogs and placed all but two of these in the Cystignathidae. *Cryptotis (=Adelotus)* was placed in the Asterophrydidae and *Thoropa* in the Hylidae. Cope placed the other 35 genera in six subfamilies, two of which (Criniae and Pleurodemae) were new. Cope recognized the Ceratophrydes *(Ceratophrys, Chiroleptes,*

Limnomedusa, Stombus, Tomopterna, and *Zachaenus),* Criniae *(Alsodes, Borborocaetes, Crinia, Cycloramphus, Eusophus, Helioporus, Hyperoleia, Neobatrachus,* and *Platyplectrum),* Cystignathi *(Cystignathus, Gnathophysa, Gomphobates,* and *Tarsopterus),* Hylodes *(Enhydrobius, Epirhexis, Hylodes, Limnocharis, Lithodytes, Phyllobates,* and *Strabomantis),* Pleurodemae *(Hylorhina, Liuperus,* and *Pleurodema)* and Pseudes *(Mixophyes, Pithecopsis, Lysapsus* and *Pseudis).* The genera *Batrachyla, Nattereria, Plectromantis,* and *Telmatobius* were included in the Cystignathidae but not assigned to any of the six subfamilies. Noble (1931) used Cope's Criniae (as Criniinae) for all Australo-Papuan leptodactylids, and the classification he put forth bears sufficient resemblance to Cope's (1866) that it seems reasonable to assume that Cope's classification served as Noble's prototype.

Mivart (1869) attempted to integrate the two classifications proposed by Günther (1859a) and Cope (1866) but in my opinion did not contribute to a better understanding of anuran relationships. He continued the use of two unreliable characters—reduction (or loss) of the auditory apparatus and loss of maxillary teeth. He placed 38 leptodactylid genera in 9 families and proposed several new (and unnecessary) subfamily names—*Pseudophryne* was placed in the Phryniscidae (Phryniscina); *Adenomera, Chelydobatrachus,* and *Paludicola* in three subfamilies (Engystomina, Brevicipitina, and Paludicolina) of the Engystomidae; *Alsodes* and *Telmatobius* in the Alsodina and *Cacotus* in the Cacotina, both subfamilies of the Bombinatoridae; *Plectromantis* was the only member of the Plectromantidae; *Hyperolius* (=*Uperoleia, nec* Rapp, 1842), *Helioporus,* and *Nattereria* in the subfamily Uperoliina (Alytidae); *Thorpa* in the Hylidae; *Leiyla* in the Acridina and *Crossodactylus, Elosia, Epirhexis, Hylodes,* and *Strabomantis* in the Hylodina (Polypedatidae); *Odontophrynus* was placed in the Ranina (Ranidae) and *Ceratophrys, Crinia, Cycloramphus, Cystignathus, Eusophleus* (=*Eupsophus), Hylorhina, Leiuperus, Limnocharis, Limnodynastes, Mixophyes, Neobatrachus, Pithecopsis, Platyplectrum, Pleurodema,* and *Zachaenus* in the Cystignathina (Ranidae); and four genera were placed in the Discoglossidae, *Calyptocephalus* and *Chiroleptes* (Chiroleptina), *Cryptotis* (Asterophrydina) and *Grypiscus* (Grypiscina). Of these family group names, six were new and based on leptodactylids—Alsodina, Cacotina, Chiroleptina, Grypiscina, Paludicolina, and Plectromantidae. Parker (1940) pointed out that the Chiroleptina cannot be used because the type genus is a homonym; this was the only family group name proposed for the group Parker (1940) named the Cycloraninae. Paludicolina and Plectromantidae are synonymous with the Leptodactylinae. Alsodina and Cacotina are based on type genera which are synonymous (Lynch, 1968b) with *Eupsophus* but are otherwise available and older names for Gallardo's (1965) Batrachylinae. Grypiscina is based on *Grypiscus,* a synonym of *Cycloramphus,* and thus is an older name for Lutz's (1954) Cycloramphinae.

Boulenger (1882) recognized 34 genera of leptodactylids and placed these in seven families—*Grypiscus* (Amphignathodontidae), *Engystomops, Myobatrachus, Notaden,* and *Pseudophryne* (Bufonidae), *Batrachophrynus* (Dendrophryniscidae), *Adenomera* (Engystomatidae), *Thoropa* (Hylidae), *Batrachopsis* and *Ranaster* (Pelobatidae), and 28 genera (two were members of other families) in the Cystignathidae [*Alsodes, Borborocoetes, Calyptocephalus, Ceratophrys, Chiroleptes, Crinia, Cryptotis, Cyclorhamphus, Edalorhina, Elosia, Heleioporus, Hylodes, Hylorhina, Hyperoleia, Leptodactylus, Limnodynastes, Limnomedusa, Mixophyes, Nattereria, Paludicola, Phyllobates* (in the sense of *Syrrhophus*), *Plectromantis, Telmatobius,* and *Zachaenus].* Many of the gen-

era proposed by previous authors were combined with the genera he recognized, the first major step toward a synthetic classification. Boulenger recognized no subfamilies of Cystignathidae.

Noble's (1931) classification combined two large families (Bufonidae and Leptodactylidae), and he recognized five subfamilies for the leptodactylids—Criniinae, Elosiinae, Heleophryninae, Leptodactylinae, and Pseudinae. Only *Sminthillus* was erroneously associated (Brachycephalidae), although *Pseudis* was included in the Leptodactylidae.

Several additional works of limited geographic coverage are of significance. In his study of the Brasilian frogs, Miranda-Ribeiro (1926) recognized six families of leptodactylids—Ceratophrydidae, Elosiidae (new), Hylodidae, Leptodactylidae, Paludicolidae, and Telmatobiidae. More significant, however, was a paper by Parker (1940) in which he analyzed the variation in the Australo-Papuan leptodactylids (Criniinae of Noble, 1931; Davis, 1936) and recognized two subfamilies, the Cycloraninae (new) and the Myobatrachinae. The acceptance of these two well-defined groups has been delayed because too little has been known of the African and American genera.

Lutz (1954) proposed two subfamilies, Cyclorhamphinae and Eleutherodactylinae, and placed a single genus in each, although in later papers she expanded the groups. Gallardo (1965) emended the Cyclorhamphinae to Cycloramphiinae, but both authors were apparently unaware of Mivart's (1869) Grypiscina. Reig (1960a) concluded that *Calyptocephalella* (=*Caudiverbera*, Myers, 1962) was not so closely related as had been previously supposed to the other telmatobiine frogs and named the Calyptocephalellinae.

Gallardo (1965) attempted to arrange all of the Neotropical leptodactylids in subfamilies and proposed two new subfamilies. Unfortunately he did not assign all of the genera to subfamilies, and several of his associations are highly heterogeneous and unnatural. The subfamilies he recognized are: Batrachylinae (new, but synonymous with Mivart's Alsodina and Cacotina), Ceratophryinae, Cycloramphiinae (synonymous with Mivart's Grypiscina), Eleutherodactylinae, Elosinae, Leptodactylinae, Pseudopaludicolinae (new), and Telmatobiinae.

Perhaps the most different classification of the Leptodactylidae at the family-level is that of Kuhn (1965). His Leptodactylidae included six subfamilies —Elosiinae, Ceratophryinae, Calyptocephalellinae, Telmatobiinae (erroneously credited to Vellard), Cystignathinae, and Criniinae. He recognized the families Ceratophrynidae (although he also listed it as a leptodactylid subfamily one page earlier) and Heleophrynidae. He considered *Myobatrachus* the sole member of the Myobatrachinae which he placed as a subfamily of the Bufonidae.

The most recent compilation of names in the family (Gorham, 1966) is especially important because it includes all but one generic name (valid or not) proposed for leptodactylid frogs as well as about 98 percent of the specific names proposed prior to 1963. Gorham recognized 63 genera and 598 species in the family; a few genera have since been named. Many others are considered invalid by me; numerous additional species have been named, and others have been synonymized since Gorham ceased to accumulate data (1963).

One hundred and sixty-one generic names have been proposed for the 57 Recent genera recognized here (Table 2). Of the recognized genera, 50 per cent contain one or two species. The 57 genera considered by me to belong to the family Leptodactylidae are distributed over much of the southern land masses of the world (excepting Antarctica). The seventeen Australo-Papuan genera are here placed in two subfamilies (those of Parker, 1940), one of which is further subdivided into two

TABLE 2. Generic names of leptodactylid frogs and the corresponding generic names used here.

Name proposed	Name used herein
Adelotus Ogilby, 1907	*Adelotus*
Adenomera Steindachner, 1867	*Leptodactylus*
Alsodes Bell, 1843	*Eupsophus*
Amblyphrynus Cochran & Goin, 1961	*Amblyphrynus*
Barycholos Heyer, 1969	*Barycholos*
Basanitia Miranda-Ribeiro, 1923	*Eleutherodactylus*
Batrachophrynus Peters, 1873	*Batrachophrynus*
Batrachopsis Boulenger, 1882	*Lechriodus*
Batrachyla Bell, 1843	*Batrachyla*
Borborocaetes Cope, 1866	*Eupsophus*
Borborocoetea Strand, 1928	*Eupsophus*
Borborocoetes Bell, 1843	*Eupsophus*
Bubonias Cope, 1874	*Edalorhina*
Bufonella Girard, 1853	*Pseudophryne*
Cacotus Günther, 1868	*Eupsophus*
Calamobates deWitte, 1930	*Crossodactylus*
Calyptocephala Nieden, 1923	*Caudiverbera*
Calyptocephalella Strand, 1928	*Caudiverbera*
Calyptocephalus Dum. & Bib., 1841	*Caudiverbera*
Camariolius Peters, 1863	*Crinia*
Caudiverbera Laurenti, 1768	*Caudiverbera*
Ceratophrys Wied, 1824	*Ceratophrys*
Chacophrys Reig & Limeses, 1963	*Ceratophrys*
Cheiroleptes Spencer, 1901	*Cyclorana*
Chelydobatrachus Günther, 1859	*Myobatrachus*
Chiroleptes Günther 1859	*Cyclorana*
Cophaeus Cope, 1889	*Telmatobius*
Cornufer Tschudi, 1838	*Eleutherodactylus*
Craspedoglossa Müller, 1922	*Zachaenus*
Craugastor Cope, 1862	*Eleutherodactylus*
Crinia Tschudi, 1838	*Crinia*
Crossodactylodes Cochran, 1938	*Crossodactylodes*
Crossodactylus Dum. & Bib., 1841	*Crossodactylus*
Cryptotis Günther, 1863	*Adelotus*
Ctenocranius Melin, 1941	*Eleutherodactylus*
Cyclocephalus Jiménez de la Espada, 1875	*Eleutherodactylus*
Cycloramphus Tschudi, 1838	*Cycloramphus*
Cyclorana Steindachner, 1867	*Cyclorana*
Cyclorhamphus Agassiz, 1846	*Cycloramphus*
Cystignathus Wagler, 1830	*Leptodactylus*
Edalorhina Jiménez de la Espada, 1870	*Edalorhina*
Eleutherodactylus Dum. & Bib., 1841	*Eleutherodactylus*
Elosia Tschudi, 1838	*Hylodes* Fitz., 1826
Engystomops Jiménez de la Espada, 1872	*Physalaemus*
Entomoglossus Peters, 1870	*Leptodactylus*
Enydrobius Wagler, 1830	*Hylodes* Fitz., 1826
Epirhexis Cope, 1866	*Syrrhophus*
Euhyas Fitzinger, 1843	*Eleutherodactylus*

TABLE 2. Generic names of leptodactylid frogs and the corresponding generic names used here.—*Continued*

Name proposed	Name used herein
Euparkerella Griffiths, 1959	*Euparkerella*
Eupemphix Steindachner, 1863	*Physalaemus*
Eupsophus Fitzinger, 1843	*Eupsophus*
Eusophus Cope, 1865	*Eupsophus*
Geobatrachus Ruthven, 1915	MICROHYLIDAE
Glauertia Loveridge, 1933	*Glauertia*
Gnathophysa Cope, 1865	*Leptodactylus*
Gomphobates Rein. & Lütk., 1862	*Physalaemus*
Grypiscus Cope, 1867	*Cycloramphus*
Hammatodactylus Fitzinger, 1843	*Eupsophus*
Heleioporus Gray, 1841	*Heleioporus*
Heleophryne Sclater, 1898	*Heleophryne*
Helioporus Gray, 1841	*Heleioporus*
Heliorana Steindachner, 1867	*Limnodynastes*
Holoaden Miranda-Ribeiro, 1920	*Holoaden*
Hydrolaetare Gallardo, 1963	*Hydrolaetare*
Hylactophryne Lynch, 1968	*Hylactophryne*
Hylodes Fitzinger, 1826	*Hylodes*
Hylodes Fitzinger, 1843 *(Auctorum)*	*Eleutherodactylus*
Hylopsis Werner, 1896	HYLIDAE *(Hyla)*
Hylorhina Agassiz, 1846	*Hylorina*
Hylorina Bell, 1843	*Hylorina*
Hyperolia Cope, 1865	*Uperoleia*
Hyperoodon Philippi, 1902	*Odontophrynus*
Hypodictyon Cope, 1885	*Eleutherodactylus*
Iliobates Fitzinger, 1867	*Physalaemus*
Iliodiscus Miranda-Ribeiro, 1920	*Cycloramphus*
Ischnocnema Rein. & Lütk., 1862	*Ischnocnema*
Kyarranus Moore, 1958	*Kyarranus*
Lechriodus Boulenger, 1882	*Lechriodus*
Leinperus Dum. & Bib., 1841	*Pleurodema*
Leiyla Keferstein, 1868	*Eleutherodactylus*
Lepidobatrachus Budgett, 1899	*Lepidobatrachus*
Leptodactylus Fitzinger, 1826	*Leptodactylus*
Limnocharis Bell, 1843	*Crossodactylus*
Limnodynastes Fitzinger, 1843	*Limnodynastes*
Limnomedusa Fitzinger, 1843	*Limnomedusa*
Limnophys Jiménez de la Espada, 1870	*Eleutherodactylus*
Liohyla Cope, 1894	*Eleutherodactylus*
Lithodytes Fitzinger, 1843	*Lithodytes*
Litopleura Jiménez de la Espada, 1875	*Limnomedusa*
Liuperus Cope, 1860	*Physalaemus*
Liyla Cope, 1869	*Eleutherodactylus*
Lystris Cope, 1868	*Pleurodema*
Macrogenioglottus Carvalho, 1946	*Odontophrynus*
Malachylodes Cope, 1879	*Syrrhophus*
Megaelosia Miranda-Ribeiro, 1923	*Megaelosia*
Metacrinia Parker, 1940	*Metacrinia*

TABLE 2. Generic names of leptodactylid frogs and the corresponding generic names used here.—*Continued*

Name proposed	Name used herein
Microbatrachylus Taylor, 1940	*Eleutherodactylus*
Microphryne Peters, 1873	*Physalaemus*
Mitrolysis Cope, 1889	*Cyclorana*
Mixophyes Günther, 1864	*Mixophyes*
Myobatrachus Schlegel, 1850	*Myobatrachus*
Nattereria Steindachner, 1864	*Physalaemus*
Neobatrachus Peters, 1863	*Neobatrachus*
Niceforonia Goin & Cochran, 1963	*Niceforonia*
Niedenia Ahl, 1923	*Cycloramphus*
Noblella Barbour, 1930	*Eleutherodactylus*
Notaden Günther, 1873	*Notaden*
Odontophrynus Rein. & Lütk., 1862	*Odontophrynus*
Oocormus Boulenger, 1905	*Zachaenus*
Opisthodon Steindachner, 1867	*Limnodynastes*
Oreobates Jiménez de la Espada, 1872	*Ischnocnema*
Paludicola Wagler, 1830	*Physalaemus*
Paratelmatobius Lutz & Carvalho, 1958	*Paratelmatobius*
Parvulus Lutz, 1930	*Leptodactylus*
Peltocephalus Bibron, 1838	*Caudiverbera*
Peralaimos Jiménez de la Espada, 1875	*Physalaemus*
Perialia Gray, 1845	*Heleioporus*
Phanerotis Boulenger, 1890	*Lechriodus*
Philocryphus Fletcher, 1894	*Heleioporus*
Philoria Spencer, 1901	*Philoria*
Phractops Peters, 1867	*Cyclorana*
Phrynanodus Ahl, 1933	*Eleutherodactylus*
Phrynoceros Bibron, in Tschudi, 1838	*Ceratophrys*
Phrynopus Peters, 1873	*Eupsophus*
Physalaemus Fitzinger, 1826	*Physalaemus*
Physalaemus Fitzinger, 1843	*Pleurodema*
Pithecopsis Günther, 1859	*Cycloramphus*
Platyplectron Peters, 1863	*Limnodynastes*
Platyplectrum Günther, 1863	*Limnodynastes*
Plectomantis Cope, 1874 (emendation?)	*Leptodactylus*
Plectromantis Peters, 1862	*Leptodactylus*
Pleurodema Tschudi, 1838	*Pleurodema*
Pristimantis Jiménez de la Espada, 1870	*Eleutherodactylus*
Proceratophrys Miranda-Ribeiro, 1920	*Proceratophrys*
Pseudobatrachus Peters, 1873	*Telmatobius*
Pseudohyla Andersson, 1945	*Eleutherodactylus*
Pseudopaludicola Miranda-Ribeiro, 1926	*Pseudopaludicola*
Pseudophryne Fitzinger, 1843	*Pseudophryne*
Pterophryne Günther, 1867	*Crinia*
Pternophrynus Lütken, 1863	*Crinia*
Ranaster MaCleay, 1878	*Limnodynastes*
Ranidella Girard, 1853	*Crinia*
Rhinoderma Dum. & Bib., 1841	RHINODERMATIDAE
Scythrophrys new genus	*Scythrophrys*

TABLE 2. Generic names of leptodactylid frogs and the corresponding generic names used here.—*Concluded*

Name proposed	Name used herein
Sibilatrix Fitzinger, 1843	*Leptodactylus*
Sminthillus Barbour & Noble, 1920	*Sminthillus*
Stombus Gravenhorst, 1825	*Ceratophrys*
Stombus (Auctorum)	*Proceratophrys*
Strabomantis Peters, 1863	*Eleutherodactylus*
Syrrhaphus Günther, 1900	*Syrrhophus*
Syrrhophus Cope, 1878	*Syrrhophus*
Syrrhopus Boulenger, 1888	*Syrrhophus*
Tarsopterus Rein. & Lütk., 1862	*Crossodactylus*
Taudactylus Straughan & Lee, 1966	*Taudactylus*
Teletrema Miranda-Ribeiro, 1937	*Eleutherodactylus*
Telmatobius Wiegmann, 1835	*Telmatobius*
Telmatobufo Schmidt, 1952	*Telmatobufo*
Thoropa Cope, 1865	*Thoropa*
Tomodactylus Günther, 1901	*Tomodactylus*
Trachyphrynus Goin & Cochran, 1963	*Eleutherodactylus*
Trigonophrys Hallowell, 1856	*Ceratophrys*
Uperoleia Gray, 1841	*Uperoleia*
Wagleria Girard, 1853	*Limnodynastes*
Zachaenus Cope, 1866	*Zachaenus*
†*Eophractus* Schaeffer, 1949	*Caudiverbera*
†*Gigantobatrachus* Casamiquela, 1959	*Caudiverbera*
†*Indobatrachus* Noble, 1930	†*Indobatrachus*
†*Neoprocoela* Schaeffer, 1949	†*Neoprocoela*
†*Wawelia* Casamiquela, 1963	†*Wawelia*

tribes. These two subfamilies might well represent, as apparently does the South African Heleophryninae, independently derived stocks of megophryine pelobatids. The Neotropical part of the family is divided into four subfamilies, one of which is further divided into five tribes. The classification I propose is as follows:

Subfamily Ceratophryinae (Neotropical).
Included genera: *Ceratophrys, Lepidobatrachus,* and the Miocene *Wawelia.*

Subfamily Cycloraninae (Australo-Papuan).
Tribe Cycloranini (included genera: *Cyclorana, Heleioporus, Mixophyes, Neobatrachus,* and *Notaden*).
Tribe Limnodynastini (included genera: *Adelotus, Kyarranus, Lechriodus, Limnodynastes,* and *Philoria*).

Subfamily Elosiinae (Neotropical).
Included genera: *Crossodactylus, Hylodes,* and *Megaelosia.*

Subfamily Heleophryninae (South African).
Included genera: *Heleophryne.*

Subfamily Leptodactylinae (Neotropical).
Included genera: *Barycholos, Edalorhina, Hydrolaetare, Leptodactylus, Limnomedusa, Lithodytes, Paratelmatobius, Physalaemus, Pleurodema,* and *Pseudopaludicola.*

Subfamily Myobatrachinae (Australo-Papuan).
Included genera: *Crinia, Glauertia,* the Eocene *Indobatrachus* (peninsular India), *Metacrinia,*

Myobatrachus, Pseudophryne, Taudactylus, and *Uperoleia.*

Subfamily Telmatobiinae (Neotropical).

Tribe Alsodini (included genera: *Batrachyla, Eupsophus, Hylorina,* and *Thoropa*).

Tribe Eleutherodactylini (included genera: *Amblyphrynus, Eleutherodactylus, Euparkerella, Holoaden, Hylactophryne, Ischnocnema, Niceforonia, Sminthillus, Syrrhophus,* and *Tomodactylus*).

Tribe Grypiscini (included genera:

Tribe Odontophrynini (included *Crossodactylodes, Cycloramphus,* and *Zachaenus*).
genera: *Odontophrynus* and *Proceratophrys*).

Tribe Telmatobiini (included genera: *Batrachophrynus, Caudiverbera,* the Oligocene *Neoprocoela, Telmatobius,* and *Telmatobufo*).

Tribe *incertae sedis: Scythrophrys.*

The justifications for the above mentioned taxonomic rearrangements and the recognition of as many or as few (depending on the reader's inclinations) as 57 Recent genera are the substance of the following account.

MATERIALS AND METHODS

In the course of this study 304 dried skeletons, 343 cleared and stained specimens, and innumerable preserved specimens were examined. In addition, four species were studied by means of stereo-radiographs. The material used in formulating the generic accounts is listed in the Appendix.

Illustrated material is identified in the legends to figures by museum and catalogue number; the abbreviations correspond to the following institutions and collections:

AMNH	American Museum of Natural History, New York
AS	Private collection of Albert Schwartz, Miami
BMNH	British Museum (Natural History), London
EHT	Private collection of Edward H. Taylor, Lawrence
FMNH	Field Museum of Natural History, Chicago
JDL	Private skeleton collection of John D. Lynch
KU	University of Kansas Museum of Natural History
LSUMZ	Louisiana State University Museum of Zoology
MCZ	Museum of Comparative Zoology, Harvard University
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum

Observations on the skeleton, which form the greater part of this study, were made by the following techniques: 1) examination of dried, dermestid-cleaned skeletons or of macerated, disarticulated skeletons; the latter were of special importance in the study of smaller species; 2) examination of cleared and stained specimens prepared by the technique described by Davis and Gore (1936); this technique was used for study of relatively small preserved specimens (less than 40 mm. snout-vent length); 3) stereo-radiographs prepared in the manner described by Smith and Smith (1967) for study of genera known only from type-specimens and/or very few specimens; 4) limited dissection used on rare species and to check relatively superficial characters in large series of specimens; this technique usually involved careful peeling back of the derm of the head and then careful separation or removal of muscle blocks; the technique was used effectively to study the arrangement and relationships of the roofing bones, squamosal architecture, and to check for the presence or absence of a frontoparietal fontanelle; and 5)

microscopic study of serial sections of the head in the manner described by Trueb (1968); this technique was used for comparisons with the works of du Toit, de Villiers, and Baldauf.

The hyolarynx, thigh and jaw musculature, and the pectoral anatomy were studied by dissection of preserved material or study of cleared and stained material.

All drawings used in the following account were prepared by me using a Wild binocular dissecting microscope with an attached drawing tube. No effort was made to correct for distortion or to idealize or improve the drawings over the condition of the specimen, inasmuch as such corrections might confound more than clarify. The species (skeletal material only) used in formulating the generic accounts are listed alphabetically in the appendix.

GENERIC CONCEPT

Early in my study, I decided that the basic unit would be the genus. Because all categories above and below the species are arbitrary, some comment on my generic concept is in order.

There are two approaches towards genera and their definition. These have been termed "typological" and "nontypological" by Inger (1958). Likewise, they might be termed "morphological" and "adaptive" approaches. There are advantages and disadvantages to each approach. The morphological approach has been, in practice, the more widely used, but as we learn more about the biology of the organisms with which we work, we are finding that most, if not all, genera have an ecological niche of sorts. This generic niche is an integral part of the adaptive approach to genera as discussed by Inger (1958).

In terms of morphology, there is a tacit philosophy that states that external characters are used in species and species-group classification, whereas osteological characters are those of genera. Although there is some measure of fact in this philosophy, it cannot be regarded as an iron-fast rule as pointed out by Inger. The single-character classification, so prevalent in many groups, is a prominent liability at the generic level in leptodactylid classification. It is most often applied to superficially similar, yet not closely related, genera such as *Ceratophrys, Odontophrynus, Proceratophrys,* and *Zachaenus.* This wide usage of one or two characters to define any leptodactylid genus has resulted in almost all leptodactylid genera being very poorly defined. Most authors have concerned themselves with the genera and species of a rather limited geographic area, such as southeastern Brasil or México, and have emphasized rather trivial characteristics as being important in generic diagnoses. Myers (1962) justifiably criticized these workers for their use of such characters as the presence or absence of prevomerine teeth or some of the body glands.

Within the order Salientia, generic concepts differ from group to group. *Amalops* and *Rana,* both Malaysian frogs, cannot be satisfactorily separated as adults, but they are very distinctive in tadpole morphology and, to a lesser extent, in ecology. This case is certainly not equivalent to the case of two other Malaysian genera, *Bufo* and *Pseudobufo,* which differ in morphology and ecology of both the adults and tadpoles. In Inger's (1958) "adaptive approach to genera" he used the Malaysian Bufonidae as his example. Within this group, and for the Bufonidae in general, Inger's generalizations are true. However, unlike the Leptodactylidae, small divergent groups of species recognized as monotypic or small genera are rare in the Bufonidae. Inger (1958) discussed many of the theoretical and practical difficulties of the generic concept. In some groups of animals, monotypic genera will be an absolute necessity even after the evolutionary trends of that group become apparent and a more synthetic approach to their classification is possible.

The Leptodactylidae were in the stage of poorly known evolutionary patterns until a few years ago. We now have a reasonably complete picture of the general evolutionary trends within the family and some, if not all, of the adaptive patterns. Therefore, one might argue, there should be little need for, or sense to, the recognition of many monotypic genera. Nevertheless, after considerable study, I still advocate the recognition of 18 monotypic genera. Of course, it is unknown how many of these will contain as yet undescribed species, but this difficulty need not concern us.

Mayr, Linsley, and Usinger (1953: 48) required that genera be units that were ". . . separated from other genera by a decided gap." Difficulties in this essentially resemblance-difference system stem from the definition of a "decided gap." These authors further suggested that the size of the gap be in inverse proportion to the size of the genera. Thus the difference between monotypic genera should be proportionately greater than the difference between medium-sized or large genera.

Genera are radiations in some cases (medium-sized and large genera) but monotypic genera, in the absence of a fossil record, cannot be referred to as radiations. Leptodactylid genera are monotypic, small (2-4 species), medium-sized (5-10 species), large (14-35 species), or very large. The last category includes only one genus, *Eleutherodactylus,* with more than 350 species. All genera, if they are to be realistic, must be morphologically distinctive as adults. I would therefore not separate *Amalops* from *Rana,* although it is desirable that genera likewise be distinctive as larvae.

All of the genera recognized here are morphologically discrete units characterized by a relatively high degree of homogeneity, in terms of both morphology and ecology. Available data, albeit incomplete, suggest that each of the genera exhibits distinctive ecological parameters. Some of these are the same among members of unrelated phyletic lines, but this does not render the generalization any less important. For example, the presence of a foam nest in the breeding biology of both *Pleurodema* and *Limnodynastes* does not mean that they are not generically distinct ecologically.

ANALYSIS OF CHARACTERS

Many biologists have gone before me in the quest of biological and morphological bases for a classification of the advanced, though generalized frogs of the family Leptodactylidae. To these pioneers I owe special thanks for their published accounts, which have served as my sources for much of the data on behavior and larval morphology. In the following discussion I have, except where circumstance dictates that use of a generic synonym is more explanatory, used the generic names that I recognize as valid in the systematic summary.

The higher classification of frogs is a source of much argument and debate. Much literature has accumulated on the subject, in general attacking proposed classifications. The most recent proposal and attack respectively are the papers by Griffiths (1963) and Inger (1967). The two divergent sets of criteria proposed by anuran systematists are 1) a system based primarily upon the nature of the pectoral girdle; the proponents have been Cope, Boulenger, and Griffiths; and 2) a system based primarily upon the nature of the vertebral centrum and the thigh musculature; the principle proponent was Noble. Neither system has a profound effect on the Leptodactylidae, although the former would in some cases align some leptodactylids with ranids. The latter system would not permit association of genera with paedomorphic vertebral centra with the families with which they belong. Furthermore, the second system does not take into ac-

count the variation in the disposition of the distal tendons of the thigh muscles.

Davis (1936), among others, used the term Bufonoidea to embrace those groups of frogs which tend to be more like the bufonids than the ranids. The recognition of the Bufonoidea and Ranoidea is a means of subdividing the more advanced frogs. This was the object of Noble's Procoela and Diplasiocoela, and Boulenger's Arcifera and Firmisterna, which approximate the Bufonoidea and Ranoidea as here used. The Bufonoidea can be defined as follows: ribs absent in both larvae and adults; *m. sartorius* present; sternum present (except in *Brachycephalus*); scapula not overlain anteriorly by lateral development of clavicle; pectoral girdle arciferal with free epicoracoidal horns, or if firmisternal, epicoracoidal horns present but fused medially or epicoracoidal horns absent (Dendrobatidae); prezonal and/or post-zonal elements lacking bony styli; vertebral centra paedomorphic or procoelous; larvae type 4 of Orton, 1953, (spiracle sinistral, beak present, labial papillae and teeth present); parahyoid bone absent; arytenoid cartilage lacking apical cartilages; glandular pharyngeal folds lacking.

The Bufonoidea includes the following families: Bufonidae (including the Atelopodidae *auctorum*), Centrolenidae, Dendrobatidae, Hylidae, Leptodactylidae, and Pseudidae. The Leptodactylidae are regarded as the basal stock from which all other families of Bufonoidea have evolved. The Atelopodid-Bufonid line differs by the presence in the adult (or in the young) of an organ of Bidder. The families differ from one another in only the mesial fusion of the epicoracoidal halves of the pectoral girdle. Dr. Roy McDiarmid has recently completed an osteological study of the family Atelopodidae and considers it inseparable from the Bufonidae—a position with which I concur on the basis of my own observations. The Hylidae, Centrolenidae, and Pseudidae differ from the other three families in the possession of an intercalary phalangeal element. It is elongate and bony in the pseudids and short and cartilaginous in the centrolenid-hylid complex. The occipital condyles of the pseudids, hylids, and centrolenids are widely separated and stalked. The centrolenids are the only bufonoid frogs exhibiting fusion of the astragalus and calcaneum and uniform T-shaped terminal phalanges throughout the family. T-shaped terminal phalanges occur in several bufonids and leptodactylids, and in the dendrobatids. The omosternum is lost in all centrolenids but is retained by at least some members of all other families. The dendrobatids are the only bufonids with a truly firmisternal pectoral girdle. They further differ in the loss of both the prevomers and the palatines. The Leptodactylidae are defined as the remaining bufonoid frogs. All lack an organ of Bidder, intercalary phalangeal element (cartilages or bone), and have an arciferal or modified arciferal pectoral girdle (the epicoracoidal horns are visible near the posterior edge of the sternum).

Few characteristics are demonstrably primitive in the Anura. Frogs are unquestionably amphibians but the lack of a fossil record makes it difficult or impossible to relate them to any fossil group. Parsons and Williams (1962, 1963) presented convincing evidence supporting the idea that the three living amphibian orders are more closely related to one another than any one is related to some extinct amphibian order. Thus characteristics which are shared by a few anuran groups and most other Lissamphibia are more likely to be primitive than a character unique to the order Anura. The presence of free ribs (in the adult or larva) is therefore a primitive character in frogs as are the following: high number of presacral vertebrae, imbricate neural arches, arciferal pectoral girdles, fully aquatic larvae, and the retention of tail muscles. These characteristics (here termed first

degree) occur in some or all of the archaic frog families (Ascaphidae, Discoglossidae, Pipidae, and Rhinophrynidae) as well as in a few of the advanced families.

Another set of characteristics (second degree) are usually not evident (or difficult to homologize) in non-anurans and are largely restricted to the archaic frog families, but occur in some advanced families (principally the Pelobatidae but sometimes in leptodactylids). Because this set of characteristics is associated (correlated) with the distribution of first degree characteristics, the second degree characteristics may be reasonably asserted to be primitive. Inguinal amplexus, the presence of a parahyoid, and the absence of a discrete *m. sartorius* are second degree characteristics.

First and second degree characteristics are therefore considered primitive throughout this study. Following the reasoning of Sporne (1954), I also recognize a third set of characteristics as primitive because the distribution of these characteristics among frogs is correlated with the distribution of the first and second degree characteristics. Third degree characteristics are usually apparent in some of the archaic frog families and are always apparent in the Pelobatidae. The following characteristics are third degree characteristics: 1) occipital condyles large and closely approximated medially, and cervical cotyles closely approximated medially; 2) transverse processes of anterior presacral vertebrae elongate and transverse processes of posterior presacral vertebrae shortened; 3) sacral diapophyses broadly dilated; 4) sacral vertebrae with postzygapophyses and coccyx with prezygapophyses; 5) intervertebral discs free; 6) pupil vertical; 7) outer metatarsal tubercle absent; 8) tadpole with median vent; and 9) tadpole dental formula including at least three rows anterior to and three rows posterior to the beak. These nine character states are considered primitive.

NON-OSTEOLOGICAL CHARACTERS

A number of morphological and non-morphological character complexes or traits are considered here. Some of these have not previously been given serious consideration, whereas others have been afforded considerable weight in the construction of classifications.

Early classifications utilized obvious, ecologically adaptive characters, such as are used by the layman today. The "frog" versus "toad" classification is still prevalent and is (and was) based largely on the presence or absence, respectively, of webbing on the digits of the hind limb. Within the leptodactylids examples of the "frog" would be *Cycloramphus, Paratelmatobius,* or *Telmatobius* in the Neotropics and *Cyclorana* and *Mixophyes* in the Australo-Papuan region. The "frog-toad" classification also used pustularity of the skin, the presence of parotoid glands, and environmental preference (field or pond). Abundant evidence has been presented refuting such a classification. Nonetheless, a number of behavioral and externally apparent morphological features can be investigated for possible use in constructing phylogenies and classifications. Among such features discussed below are the following: amplectic position, larval characteristcis, developmental patterns, breeding sites and nests, secondary sexual features of the male (vocal apparatus, nuptial callosities, excresences, spines), pupil shape, tongue morphology, foot morphology (webbing, metatarsal arrangement, tarsal folds), and glands on the body.

Recently, serious consideration has been revived in myological variation and taxonomic usefulness. Three major areas of concern here involve the myology of the jaw, the myology of the thigh, and the hyoid musculature. Noble (1922), Parker (1940), and Limeses (1963,

1964) contributed significantly to the study of thigh musculature. Noble used variation in the thigh musculature (especially distal thigh) to support his classification of the frogs (1922). Starrett (1968) reclassified the Anura on the basis of the jaw musculature of adults and tadpoles.

Several trends are evident in these non-osteological features, some of which are suggested below to be of phylogenetic significance. Most, however, are extremely labile features appearing independently in many lines of evolution in response to similar ecological conditions.

Amplectic Position

It is generally conceded (Tihen, 1965) that "primitive frogs" amplex in a pelvic position and that "advanced frogs" amplex in an axillary position. Few authors (Thomas, 1854, Bruch, 1863) have seriously suggested utilizing amplectic position as a major taxonomic criterion. Indeed, most authors (e.g., Boulenger, 1912, Jameson, 1955, Griffiths, 1963) stressed the variability of amplectic position and ruled the character useless in ascertaining relationships. For example, in breeding congresses of toads *(Bufo)*, males can be found amplexing females anterior to, above, or a variable distance behind the arms; all of these variations are minor, temporary, or fortuitous deviations from the axillary amplectic pattern characteristic of the Bufonidae. Tihen (1965) suggested that the transition from a pelvic to an axillary amplectic position was an evolutionary trend but noted that individual genera may deviate to a highly specialized degree. The genus most often cited is *Alytes*. *Alytes*, unlike other discoglossid frogs *(Barborula, Bombina,* and *Discoglossus)*, is usually characterized as having cephalic amplexus instead of the pelvic amplexus seen in the other genera. The cephalic amplexus of *Alytes* is a post-fertilization specialization on the part of the male for entwining the egg strings about his hind legs where the early development ensues. Just prior to and often during fertilization, *Alytes*, like other discoglossids, engages in pelvic amplexus (Boulenger, 1897).

Since Jameson's (1955) review of breeding behavior in the Anura, amplectic pattern data have been gathered for examples of all but one family (Sooglossidae) and for many more genera of frogs. We find the following distribution of pre-fertilization amplectic patterns (pelvic or axillary) in fourteen families of frogs (not all genera or species have been observed in all families, but based on available observations, these families can be characterized as either pelvic or axillary):

Pelvic amplexus:
- Ascaphidae
- Discoglossidae
- Pipidae
- Rhinophrynidae
- Pelobatidae
- Leptodactylidae (part)

Axillary amplexus:
- Bufonidae
- Centrolenidae
- Hylidae
- Pseudidae
- Leptodactylidae (part)
- Microhylidae
- Ranidae
- Hyperoliidae

The evolutionary trend suggested by Tihen (1965)—pelvic to axillary amplexus—is reasonable. Fewer sperm are probably required when the male and female gametes are released in close proximity. Some pelvic amplexing frogs have specialized their breeding behavior to compensate for their less efficient amplectic type. *Ascaphus* has an intromittent organ, the "tail"; pipids have a "flip-over" fertilization cycle (Rabb and Rabb, 1960, 1963a, 1963b). Most of the slight variation in clasping position probably reflects modifications brought about by selection for greater fertilization economy. It is inconceivable that there is any

selective advantage in shifting from axillary to pelvic amplexus. Were there any advantage, it would probably be evident by the occurrence of some bufonids, hylids, or ranids exhibiting pelvic amplexus.

As is evident by examination of the above table, only the Leptodactylidae exhibit both axillary and pelvic amplexus (Fig. 2). All other families are uniformly axillary or pelvic amplexing frogs.

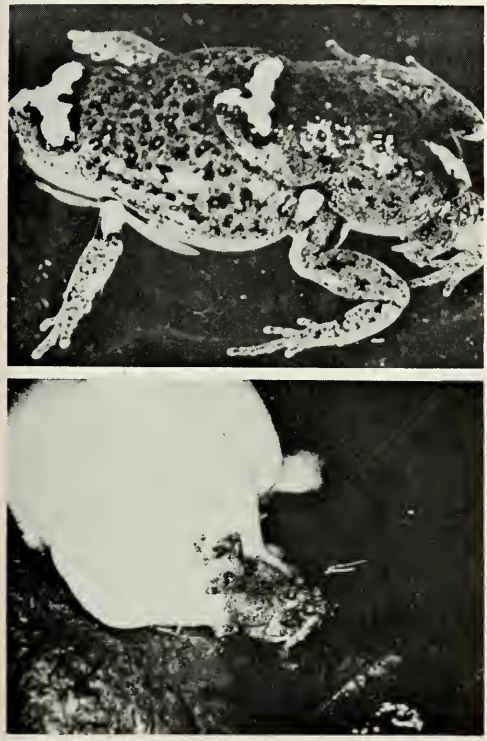

FIGURE 2. Amplexing pairs of *Pseudophryne australis* (top) and *Physalaemus pustulosus* (bottom); the latter also illustrates a foam nest. Photo of *Pseudophryne* courtesy of John A. Moore; that of *Physalaemus* courtesy of William E. Duellman.

Amplexus has not been observed (or reported) in the following leptodactylid genera: *Amblyphrynus, Barycholos, Crossodactylodes, Edalorhina, Heleophryne, Hydrolaetare, Ischnocnema, Lithodytes, Megaelosia, Myobatrachus, Niceforonia, Notaden, Scythrophrys, Taudactylus, Telmatobufo,* and *Thoropa.*

The following genera have been observed to engage in pelvic amplexus: *Adelotus, Batrachyla, Crinia, Cyclorana, Glauertia, Heleioporus, Kyarranus, Lechriodus, Limnodynastes, Metacrinia, Mixophyes, Neobatrachus, Philoria, Pseudophryne,* and *Uperoleia.* The only variations known within these genera are the report of Fletcher (1889) that *Mixophyes* engages in axillary amplexus (M. J. Littlejohn and A. A. Martin observed only pelvic amplexus in this genus), and a photograph of an axillary amplexing pair of *Batrachyla taeniata* sent to me by José Cei (Barrio, 1967a, observed only pelvic amplexus in the other two species of the genus).[1]

The following genera have been observed to engage in only axillary amplexus: *Batrachophrynus, Caudiverbera, Ceratophrys, Crossodactylus, Cycloramphus, Eleutherodactylus, Euparkerella, Eupsophus, Holoaden, Hylactophryne, Hylodes, Hylorina, Lepidobatrachus, Leptodactylus, Limnomedusa, Odontophrynus, Paratelmatobius, Physalaemus, Pleurodema, Proceratophrys, Pseudopaludicola, Syrrhophus, Telmatobius, Tomodactylus,* and *Zachaenus.*

Examination of these lists immediately points out that no Australo-Papuan genus exhibits axillary amplexus (if we dismiss Fletcher's, 1889, report) and only one Neotropical genus exhibits pelvic amplexus. The Australo-Papuan leptodactylids are judged to be closely related to megophryine pelobatids, based on morphology, and the primitive amplectic pattern corresponds with this close relationship. In view of the wide distribution of pelvic amplexus in the Australo-Papuan leptodactylids and the probable irreversibility of this evolutionary trend, I consider the Australo-Papuan leptodactylids to have primitively exhibited pelvic amplexus.

All but one *(Batrachyla)* of the 26

[1] Dr. Ian Straughan *(in litt.)* suggested that all cycloranines employ axillary amplexus. He has observed axillary amplexus in several taxa. His observations are contrary to observations published by Littlejohn (1963), Martin (1968), and Moore (1961).

Neotropical leptodactylid genera for which pre-fertilization amplectic positions are known exhibit axillary amplexus. The large number of genera with axillary amplexus and their diversity suggests that the shift to axillary amplexus was made early in the evolution of the Neotropical leptodactylid stock, because each time a shift occurs independently, it is less likely that the frogs of a given amplectic type are related. For example, if of 20 genera (all judged closely related), one exhibited pelvic amplexus and the other 19 axillary amplexus, it is more likely that the shift occurred only once (prior to the evolution of the 19 axillary amplexing genera) and not that it may have occured independently two, 10, or 19 times. The occurrence of a single pelvic amplexing genus of Neotropical leptodactylids is witness either to the primitive stock exhibiting pelvic amplexus, or the invasion of two stocks, one having pelvic amplexus and the other axillary amplexus.

It is not unlikely that isolated phyletic lines could have achieved the axillary grade independently. Such units as *Heleophryne*, *Rhinoderma* or the sooglossid ranoids may have independently evolved axillary amplexus. Data are not available for *Heleophryne* or the sooglossid ranoids, but each group exhibits many primitive characteristics and could have either pelvic or axillary amplexus.

Breeding Behavior and Development

Many authors have reported on the direct development of frogs of the genus *Eleutherodactylus*. Most other frogs typically lay the eggs in water and have a free-swimming larval stage. Of the "typical frogs" some construct a foam or froth nest in which the earliest development of the tadpole takes place. Leptodactylid frogs can be divided into three classes: those laying the eggs directly in water, those depositing the eggs in a foam nest, and those with direct development. The first group can be subdivided into those laying their eggs in ponds and slow streams or rivers (most species) and those laying their eggs in close association with torrential mountain streams (e.g., *Heleophryne* and *Thoropa*). Within the group that builds foam nests some species deposit the eggs in a nest built in moist terrestrial situations which are later flooded (e.g., *Heleioporus* and members of the *Leptodactylus fuscus* group); others deposit the eggs in a foam nest (Fig. 2) floating on water (e.g., most limnodynastine Cycloraninae, many *Leptodactylus*, *Physalaemus*, and *Pleurodema*).

No data on breeding biology or development are known for the following genera: *Amblyphrynus*, *Glauertia*, *Hydrolaetare*, *Ischnocnema*, *Limnomedusa*, *Lithodytes*, *Notaden*, *Paratelmatobius*, *Taudactylus*, and *Telmatobufo*. Only incomplete data are available for several other genera.

Batrachophrynus, *Caudiverbera*, *Ceratophrys*, *Crinia* (part), *Crossodactylus*, *Cyclorana*, *Eupsophus*, *Hylodes*, *Hylorina*, *Lepidobatrachus*, *Megaelosia*, *Mixophyes*, *Neobatrachus*, *Odontophrynus*, *Proceratophrys*, *Pseudopaludicola*, *Pseudophryne* (part), *Telmatobius*, and *Uperoleia* lay their eggs in water without building a foam nest. *Glauertia* and *Notaden* probably also lay their eggs in water (Main and Storr, 1966; Slater and Main, 1963). *Batrachyla*, *Thoropa*, and some *Crinia* and *Pseudophryne* lay their eggs in moist situations and, upon hatching, the tadpoles enter water. The same pattern is inferred for *Heleophryne*, but field observations are not available.

Adelotus, *Lechriodus*, *Leptodactylus* (*fuscus*, *ocellatus*, and *pentadactylus* groups), *Limnodynastes*, *Physalaemus* (including *Engystomops* and *Eupemphix*), and *Pleurodema* lay their eggs in foam nests floating on the surface of water. *Heleioporus*, *Kyarranus*, members of the *Leptodactylus marmoratus* group, and *Philoria* lay their eggs in foam nests in moist, terrestrial situations; development is direct in *Kyarranus* and the *L. marmoratus* group and may be in

Philoria but is not in *Heleioporus*. In *Heleioporus*, as in the *Leptodactylus fuscus* group, the eggs are laid in a foam nest in a terrestrial situation, but prior to hatching the nest is flooded and the tadpoles emerge in an aquatic environment. In the foam-nest builders, the females of *Adelotus*, *Lechriodus*, *Limnodynastes*, as well as *Kyarranus* and *Philoria* (Moore, 1958, 1961; Littlejohn, 1963), have broad, fleshy flanges on the inner fingers (cf. Fig. 48). Flanges are lacking in the other foam-nest builders. In those genera with flanged fingers that lay the eggs in a nest floating on water, the female churns a mucous in water with her hands and traps air bubbles in the froth. In *Leptodactylus*, *Physalaemus*, and *Pleurodema* the male kicks in a mucous and water mixture to trap air bubbles. The mode of building the nest in *Heleioporus* is unknown; in *Kyarranus* and *Philoria*, nest-building is accomplished by the female using the hands but not in water. Members of the *Leptodactylus marmoratus* group lay the eggs in a froth nest in a cavity (usually a hole dug in moist soil), and the embryos develop without a free-swimming tadpole stage (Heyer, 1969a).

Cycloramphus and *Zachaenus* deposit their large eggs amidst wet leaves (terrestrial situation), and development proceeds within the egg. In contrast to eleutherodactyline frogs, the egg hatches as an advanced tadpole, and the tadpole lives in the wet leaves for a short period and then metamorphoses (Lutz, 1944). *Crossodactylodes* lay their large eggs in the axillae of terrestrial bromeliads. The tadpoles complete development in the moist axillae.

Direct development (without a foam nest) occurs in *Eleutherodactylus*, *Euparkerella*, *Holoaden*, *Hylactophryne*, *Sminthillus*, *Syrrhophus*, and *Tomodactylus*, and probably also occurs in *Niceforonia* (Goin and Cochran, 1963) and *Metacrinia and Myobatrachus* (Parker, 1940). In this group development proceeds within the egg membrane, and on hatching, a miniature froglet emerges (Goin, 1946, Griffiths, 1959, Lynn, 1942, Lynn and Lutz, 1946a, 1946b, Lutz, 1958, Noble, 1926a, and Valett and Jameson, 1961). The oviducal eggs in every case are large and few in number.

The habit of building a foam nest probably has developed independently on different continents. In those Australo-Papuan genera which build foam nests and the females of which have spatulate fingers, the palatal osteology suggests a close relationship. The other Australian genus with a foam nest is closely allied to genera which do not build foam nests. The Neotropical foam-nest builders all possess an osseous sternal style and are unquestionably related; these genera also are distinctive in the mode of nest building in that the male kicks air into the nest (Bokermann, 1962).

Direct development has independently evolved in limnodynastine Cycloraninae *(Kyarranus* and *Philoria)*, the Myobatrachinae *(Metacrinia* and *Myobatrachus)*, the Leptodactylinae *(Leptodactylus marmoratus* group), and Telmatobiinae (the genera here placed in the tribe Eleutherodactylini).

Tadpole Morphology

The use of tadpole morphology in generic diagnoses has not gained wide acceptance chiefly because of the general lack of material of most species in collections. When tadpoles have been available, they have often provided additional evidence relative to the advisability of generic recognition (Inger, 1954, 1966). Examination of available specimens and utilization of reliable reports in the literature revealed some intriguing variation in the tadpoles of leptodactylids, especially in light of Inger's (1967) recent comment that some tadpole characters are invariate below the family level (e.g., the position of the anal opening).

The following characters were observed for each available genus: 1) posi-

sion of the anal opening; 2) tooth rows; and 3) distribution of labial papillae. In addition, some other characters were used when deemed of sufficient departure from the generalized body form to be characteristic at the generic level—for example, body form in the highly stream-adapted tadpoles of *Thoropa* (Fig. 3).

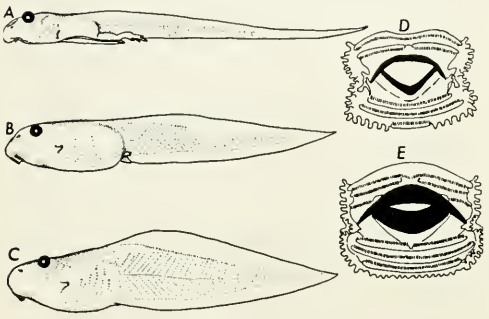

FIGURE 3. Tadpoles of (A) *Thoropa petropolitana* (KU 112394, × 4.5), (B) *Crossodactylus dispar* (after Bokermann, 1963, × 1.8), and (C) *Hylodes aspera* (KU 112387, × 1.8). Mouthparts of (D) a myobatrachine (*Crinia victoriana*, after Martin, 1965) and (E) a cycloranine (*Neobatrachus pictus*, after Martin, 1965).

Among the Neotropical genera, data are not available for *Amblyphrynus*, *Barycholos*, *Hydrolaetare*, *Ischnocnema*, *Limnomedusa*, *Lithodytes*, *Scythrophrys*, or *Telmatobufo*.[2] *Crossodactylodes* has bromeliad dwelling tadpoles (W. C. A. Bokermann, *in litt.*) and *Edalorhina* has aquatic tadpoles (R. Etheridge, *in litt.*); I have no other data for these two genera. Tadpole data are not available for the following genera, all of which have direct development: *Cycloramphus*, *Eleutherodactylus*, *Euparkerella*, *Holoaden*, *Hylactophryne*, *Niceforonia*, *Paratelmatobius*, *Sminthillus*, *Syrrhophus*, *Tomodactylus*, and *Zachaenus*. Data are available (at least in part) for each of the 18 remaining Neotropical genera that I recognize.

Tadpoles of both ceratophryine genera are known; the larvae of both genera have a median vent, highly modified tooth row formula, and relatively few, uniformly spaced papillae across the anterior edge of the mouth. *Ceratophrys* has 6/7 tooth rows and large horny beaks whereas *Lepidobatrachus* lacks larval teeth and has large but weakly developed beaks.

Data are available for four of the nine leptodactyline genera. *Leptodactylus* and *Pleurodema* have median vents, and *Physalaemus* and *Pseudopaludicola* have dextral vents. The tooth row formula for all four genera is 2/3, and the labial papillae are interrupted anteriorly.

Data are available for all three genera of the Elosiinae. *Crossodactylus* has a median vent, and *Hylodes* and *Megaelosia* have dextral vents. All three have 2/3 tooth rows and an anterior interruption in the labial papillae.

Tadpole morphology is not known for the majority of the Telmatobiinae; many of these genera exhibit direct development. Two genera depart from the typical bufonoid 2/3 tooth row formula: *Caudiverbera* has 3/3 tooth rows, and *Hylorina* has 2/2. Only one genus differs in the pattern of the labial papillae; *Batrachyla* has a complete row of labial papillae across the anterior edge of the mouth. All other genera for which data are available have an interruption anteriorly. None has a posterior interruption.

Batrachyla, *Eupsophus*, *Hylorina*, *Proceratophrys*, and *Thoropa* have median vents, whereas dextral vents occur in *Batrachophrynus*, *Caudiverbera*, *Odontophrynus*, and *Telmatobius*.

Cycloramphus and *Zachaenus* have an abbreviated larval life but do not exhibit the direct developmental pattern such as is seen in *Eleutherodactylus*. During development in the former two genera, the vent is medial and the tooth

[2] Tadpoles are now known for *Telmatobufo*. The mouth is ventral, the tooth row formula 2/3, and the papillae form a complete series around the mouth. The tadpoles are swift-stream adapted.

row formula is 1/1. The upper row of teeth is interrupted medially as in many other leptodactylids.

Tadpoles of the Australo-Papuan genera are relatively well known through the efforts of Moore (1961) and Parker (1940). Data are not available for the myobatrachine genera *Glauertia, Metacrinia, Myobatrachus,* or *Taudactylus.* At least two of these *(Metacrinia* and *Myobatrachus)* probably lack a free-living tadpole (Parker, 1940).

Two of the cycloranine genera exhibit modified developmental patterns—*Kyarranus* and *Philoria.* Both build a foam nest and lay large eggs in a terrestrial situation (Moore, 1958, 1961; Littlejohn, 1963). These genera have median anal openings as tadpoles. Reports in the literature concerning the other cycloranines are contradictory. Martin (1965), in the most recent studies on these frogs, reported median vents in *Neobatrachus pictus* and three species of *Limnodynastes (dorsalis, peronii,* and *tasmaniensis).* Moore (1961) also reported median vents in *L. dorsalis* and *L. peronii* but characterized *Neobatrachus pictus* as having a dextral vent. Parker (1940), in contrast to reports by Martin and Moore, reported a dextral vent in a *Limnodynastes (L. spenceri).* Parker (1940) and Moore (1961) provided descriptions of the larvae of *Adelotus brevis, Cyclorana platycephalus, Heleioporus eyeri, Lechriodus fletcheri,* and *Mixophyes fasciolatus,* all of which were characterized by having a dextral vent. Lee (1966) reported intraspecific variation (median or dextral) in one species of *Heleioporus*; most species of the genus have dextral vents. The cycloranines have three rows of teeth behind the beak. *Adelotus, Cyclorana,* and *Lechriodus* have 2/3 tooth rows insofar as they are known but *Heleioporus, Mixophyes, Limnodynastes, Neobatrachus,* and *Notaden* have 3/3 to 6/3 tooth rows. The labial papillae are not interrupted anteriorly in *Mixophyes* and are only narrowly interrupted in *Adelotus,* whereas there is a broad interruption in all other genera and species

Data are available for three myobatrachines—*Crinia, Pseudophryne,* and *Uperoleia.* These three genera are distinctive among leptodactylids (and most bufonoids) in having the labial papillae interrupted both anteriorly and posteriorly (Fig. 3). *Crinia* and *Pseudophryne* have 2/3 tooth rows, whereas *Uperoleia* has 1/3.

Intrafamilial varition in the position of the vent was denied by Inger (1967); however, the above data clearly indicate that variation occurs within subfamilies and even within genera and species. Starrett (1967) reported that some species of *Bufo* have a dextral vent, whereas most have a median vent, as do members of other genera in the family *(Ansonia, Atelopus,* and *Melanophryniscus). Dendrophryniscus brevipollicatus* also has a dextral vent; data are not known for the other three species of that genus, some of which are only tentatively retained in the genus.

The tadpole of the ancestral leptodactylid probably exhibited the following characteristics: 1) median vent; 2) more than 2/3 tooth rows; 3) labial papillae not or only narrowly, interrupted anteriorly, but not posteriorly; and 4) relatively deep body with high fins on the tail (deduced because the primitive leptodactylid frog was a pond breeder). Based on my analysis of the relationships of the genera, I consider the dextral vent to have appeared no fewer than five times in the course of the evolution of the American genera and no less than twice in the evolution of the Australo-Papuan genera.

The tadpole of *Heleophryne* is very specialized. The beak has been lost as in *Lepidobatrachus,* the vent is median, and the tooth rows vary from 4/11 to 4/17. The labial papillae are complete anteriorly.

Secondary Sex Characters

The development or absence of some of the secondary sex characteristics has been used in defining genera. Liu (1936) and Noble (1931) published reviews of the secondary sex characters in frogs, and Parker (1940) made some interesting speculations on the variation in nuptial excrescences. Of the numerous secondary sex characteristics that could be discussed here, the vocal pouches or sacs and the development of nuptial excrescences of the male are the most important.

The nuptial excrescences on the thumb (and sometimes second finger) vary from roughened, sandpaper-like patches, through small, numerous, closeset spines, to a few large, horny spines. Large heavy spines are uncommon in leptodactylids—*Heleioporus* and some species groups of *Leptodactylus (melanonotus, ocellatus,* and *pentadactylus)* have thumb spines. I have observed relatively little intrageneric variation in the presence or absence of nuptial asperities in leptodactylids, although this variation does occur. Parker (1940) pointed out that apparently those frogs which clasp on land and not in water lack nuptial excrescences, whereas those that clasp in water have them. This hypothesis was put forth following a study of the Australo-Papuan leptodactylids, but he did not say whether the hypothesis was formulated only on the basis of Australo-Papuan leptodactylids, or whether it was influenced by his wide experience with frogs from all over the world. Nonetheless, those genera of Neotropical leptodactylids lacking nuptial excrescences all clasp on land; most also exhibit direct development. *Kyarranus,* an Australian genus exhibiting direct development, does not clasp in water and has nuptial excrescences (Moore, 1958, 1961). A Neotropical genus, *Batrachyla,* has nuptial excrescences but clasps on land (Barrio, 1967a; Cei, 1962a). There seems to be evidence for and against Parker's suggestion. In some cases the secondary sex characters seem to have significance in suggesting relationships (e.g., within the Eleutherodactylini), but in others the characters reflect breeding behavior. This is especially apparent in *Leptodactylus,* in which the species of the two groups that clasp on land *(fuscus* and *marmoratus)* lack spines, and the three that clasp in water *(melanonotus, ocellatus,* and *pentadactylus)* have spines. The species of the *melanonotus, ocellatus,* and *pentadactylus* groups are closely related. The species of the *fuscus* group are more closely related to the groups with thumb spines than to the other group *(marmoratus)* lacking spines (Heyer, 1969a). This example illustrates the inadvisability of applying extra weight to the taxonomic value of variations in the secondary sex characteristics when constructing frog phylogenies at or above the generic level.

Secondary sex characters have been used to characterize some genera. For example, *Heleioporus* usually has one to several large spines on the thumb of the male (one species lacks spines), whereas *Neobatrachus* always has a diffuse pad on the thumb of the male. In external appearance the frogs of these two genera are otherwise difficult to separate. Nuptial excrescences are lacking in male *Niceforonia* but present in male *Eupsophus.* These genera had previously been confused and can be separated osteologically, but only with difficulty externally.

Males of the *ocellatus* and *pentadactylus* groups of *Leptodactylus* have greatly enlarged muscles in the arm; this enlargement is osteologically supported by the development of large flanges on the humerus (Fig. 41).

A curious secondary sex characteristic is exhibited by males in some species of *Eupsophus, Leptodactylus,* and *Telmatobius,* in which clusters of horny spines develop on the chest. These spines are seasonal in appearance at

least in *Eupsophus* and may be in all of the species which have them.

Few secondary sex characteristics are developed in female frogs. The females of those frogs here placed in the Limnodynastini develop spatulate fringes on the inner digits of the hand during the breeding season (Fig. 48). The fringe enables the female more easily to make the foam nest in which the eggs are deposited. Of the five genera in this tribe, males of all species have nuptial pads. Two of the genera *(Kyarranus* and *Philoria)* exhibit direct development and do not lay their eggs in water.

Male leptodactylid frogs exhibit a wide range of variation in the condition and development of vocal pouches. Several genera lack vocal sacs (e.g., *Megaelosia*), and this character varies intragenerically (e.g., *Eleutherodactylus*). Most leptodactylids have an internal or external subgular vocal sac, but the sac is paired and ventrolateral in the *Leptodactylus fuscus* group. In *Hylodes* the vocal sacs are membranous and lateral.

Pupil Shape

A widely used "generic" character in many anuran families is the nature of the pupil—horizontally or vertically elliptical (Fig. 4). I am aware of no author who has afforded the shape of the pupil more than generic value or who has suggested that it is anything more than a handy "key character."

Several pupil shapes have been described for the leptodactylid genera (horizontal, round, horizontal with ventral angle, rhomboidal, and vertical). In most cases the specimens were preserved. Apparently pupil shape is altered by death, inasmuch as species reported as having a horizontal pupil with a ventral angle by Parker (1940) have either horizontal or vertical pupils in life (Moore, 1961, Lee, 1966). *Uperoleia* has a rhomboidal pupil when preserved but the pupil is a vertical slit in life (Main and Storr, 1966, Moore, 1961). The pupil shapes in leptodactylids are variations of two types—vertical or horizontal ellipse. The only leptodactylid genera with vertical pupils are *Caudiverbera, Heleioporus, Heleophryne, Hydrolaetare, Hylorina, Lepidobatrachus, Limnomedusa, Mixophyes, Neobatrachus,* and *Telmatobufo.*

All primitive families (Ascaphidae, Discoglossidae, Pipidae, Rhinophrynidae, and Pelobatidae) have vertical pupils, with the possible exception of *Nesobia,* a rare, megophryine pelobatid. In contrast, vertical pupils are uncommon in higher frog families. No genus of bufonids, centrolenids, dendrobatids, pseudids, rhinodermatids, or sooglossids has vertical pupils. Among the Hylidae, vertical pupils occur in only the four genera of the Phyllomedusinae *(Agalychnis, Nyctimistes, Pachymedusa,* and *Phyllomedusa),* although several other

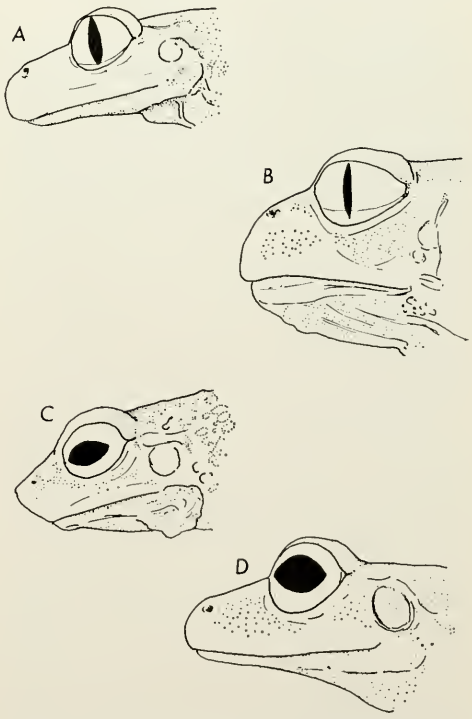

FIGURE 4. Pupil shape in (A) *Heleophryne natalensis,* KU 105923, × 2; (B) *Neobatrachus pictus,* KU 69276, × 2; (C) *Hylodes aspera,* KU 92871, × 1.5; and (D) *Eleutherodactylus silvicola,* LSUMZ 7557, × 2.5.

genera have been erroneously reported to have vertical or rhomboidal pupils.

The only microhylid genus definitely known to have vertical pupils is *Dyscophus*, although *Ctenophryne* may have vertical pupils (Parker, 1934).

Other than the Leptodactylidae, the Ranidae *(sensu lato)* are the only advanced family having several genera with vertical pupils. Ranids are diverse in terms of generic radiation except in the Americas; vertical pupils occur only in the African genera, whereas none of the several genera of ranids in the Indo-Australian Archipelago, Malaysia, and China has vertical pupils. The only ranid genera with vertical pupils belong to the group recognized as the Hyperoliidae by Laurent (1951), but several of the genera in that family group have horizontal pupils.

Hands and Feet

The degree of webbing, digital pad expansion or development, variations in the tarsal folds and tubercles, and sizes of the subarticular, supernumerary, and metatarsal tubercles have been used as generic characters in the Leptodactylidae. Within the large genera most of these characters exhibit a continuum. However, they have been used, and probably will continue to be used, to distinguish the smaller genera from the larger ones *(Eleutherodactylus* and *Leptodactylus).*

Leptodactylids are generally thought of as free-toed frogs, whereas other groups (e.g., Hylidae and Ranidae) are characteristically web-footed. The hands of all leptodactylids lack webbing; some authors have reported basal webbing of the hands, but this apparently always has been based on a poorly preserved and/or desiccated specimen. Lateral fringes are present on the digits of some species, but these cannot be interpreted as webbing. *Batrachophrynus, Caudiverbera, Ceratophrys, Cyclorana, Glauertia, Hydrolaetare, Limnomedusa, Mixophyes, Neobatrachus, Notaden, Paratelmatobius, Proceratophrys, Telmatobius,* and *Telmatobufo* have webbing between the toes; the webbing is not extensive in *Ceratophrys, Limnomedusa,* or *Proceratophrys.* Several other genera have basal webbing. Especially among the Australo-Papuan leptodactylids, the distinction between "free toes" and "webbed toes" is tenuous. The full range of webbing conditions occurs in *Cycloramphus, Eleutherodactylus,* and *Limnodynastes.*

Expanded pads occur on the tips of the digits of many leptodactylids and are apparently correlated with arboreal habits. Frogs of the genus *Eleutherodactylus* exhibit a full range of variation from terrestrial species with no pads to fully arboreal species with large, emarginate pads. The finger pads are usually larger than those on the toes but in some species the reverse is true. I previously pointed out the value and significance of the presence or absence of a terminal transverse groove on the digital pads (Lynch, 1968a). The grooves are best developed on the outer digital pads and usually better developed on the toes than on the fingers.

Boulenger (1882) used the separation or union of the outer metatarsals as a generic character. All leptodactylids are closer to the united condition than to the separated condition exemplified by *Xenopus.* Separation of the metatarsals is best developed in, but not exclusive to, those species with webbed feet. I consider the character to be of but limited importance because I find no myological basis for it in leptodactylids and find a continuum of character states relative to the separation. The separation is complete in *Mixophyes,* less so in the *Cycloramphus fulginosus* group (in which the fourth and fifth metatarsals are separated by webbing for about half of their length), and united (Fig. 5) in the web-less species of *Cycloramphus* (for example, *C. eleutherodactylus*).

The tarsus is bedecked by inner and/or outer tubercles or folds in many

leptodactylids. Usually the folds are small, often ridge-like; these folds are variable in genera and species groups and the development of the folds is sometimes sexually variable *(Eleutherodactylus rugulosus).* However, the elosiine leptodactylids have large, flap-like tarsal folds (Fig. 5) in both sexes.

The subarticular tubercles vary in size and shape. Usually they are rounded, light colored, and moderate sized, but in several species they are elongate, conical, or absent. I have not observed bifid subarticular tubercles in leptodactylids. Supernumerary plantar tubercles occur in relatively few leptodactylids and are useful in species-group and generic classification. These tubercles are arranged in rows along the metatarsals in some species, but in most they are irregularly scattered over the sole. The relative sizes of the metatarsal tubercles are of use in defining small genera and species groups in moderate sized and large genera. In a few semifossorial genera, the inner metatarsal tubercle is enlarged and spade-like (compressed and keeled).

FIGURE 5. Plantar views of feet of leptodactylid frogs. (A) *Hylodes aspera,* KU 92871; (B) *Cycloramphus eleutherodactylus,* KU 92781; and (C) *C. dubius,* KU 74196, illustrating lateral fringes on the toes, tarsal fold, and presence and absence of digital webbing. All × 1.5.

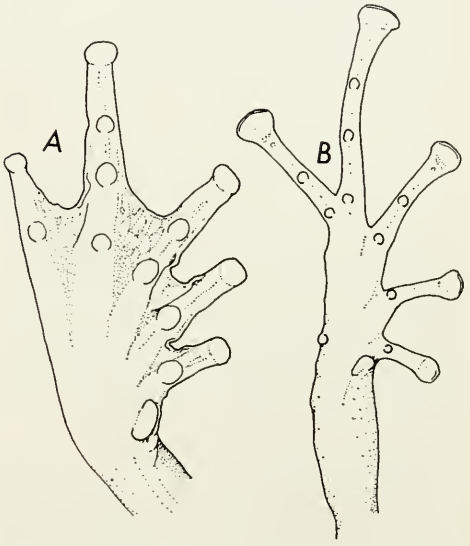

FIGURE 6. Plantar views of feet of (A) *Heleophryne natalensis* (KU 105923) and (B) *Eleutherodactylus chloronotus* (KU 117519) illustrating presence and absence of outer metatarsal tubercles. The foot of *Heleophryne* also illustrates completely separated outer metatarsals whereas those of *Eleutherodactylus* are united. × 2.

Primitive anuran families and primitive genera of the Leptodactylidae lack an outer metatarsal tubercle (Fig. 6). Many hylids and some centrolenids and ranids also lack an outer metatarsal tubercle. Within the leptodactylids I regard the development of an outer metatarsal tubercle as a derived state. Most genera with vertical pupils lack an outer metatarsal tubercle; *Uperoleia* is an exception. The development of the tubercle may be a manifestation of adaptation to terrestrial modes of life, but the generalization runs contrary to the absence of the tubercle in the fossorial pelobatid genera and *Rhinophrynus.* The presence or absence of an outer metatarsal tu-

bercle is variable in some leptodactylid genera (*Crinia, Cyclorana,* and *Limnodynastes).* The following genera lack an outer metatarsal tubercle: *Caudiverbera, Crinia* (except *georgiana, glauertia, tasmaniensis,* and the *signifera* superspecies), *Cyclorana* (except *inermis*), *Heleioporus, Heleophryne, Kyarranus, Lepidobatrachus, Limnodynastes* (except *salmini*), *Mixophyes, Neobatrachus, Notaden, Philoria, Taudactylus,* and *Telmatobufo.*

Body Glands

The presence or absence of a variety of glands on the body has been widely used in the generic classification of leptodactylids. Those glands in question are 1) paratoid, 2) lumbar, 3) inguinal, 4) tibial, and 5) flank glands. Some genera, such as *Holoaden,* are heavily glandular, whereas others lack all of the above-mentioned glands. The presence of parotoid glands is usually readily demonstrated by external examination. The same is true of the inguinal glands of some *Physalaemus* and the lumbar glands of *Pleurodema* and *Tomodactylus.* Inguinal glands usually are not clearly discernible from external examination, and their presence can be verified only by examining the inner surface of the skin. The inguinal glands vary from well defined (as in *Cycloramphus*) to loosely organized (many *Eleutherodactylus*). Schematic drawings (Fig. 7) of *Cycloramphus, Odontophrynus, Philoria, Pleurodema, Telmatobufo,* and *Uperoleia* show the most extensive development of each kind of gland.

Parker (1940) used the number of ducts of the intermaxillary glands to separate the Australo-Papuan subfamilies Cycloraninae and Myobatrachinae.

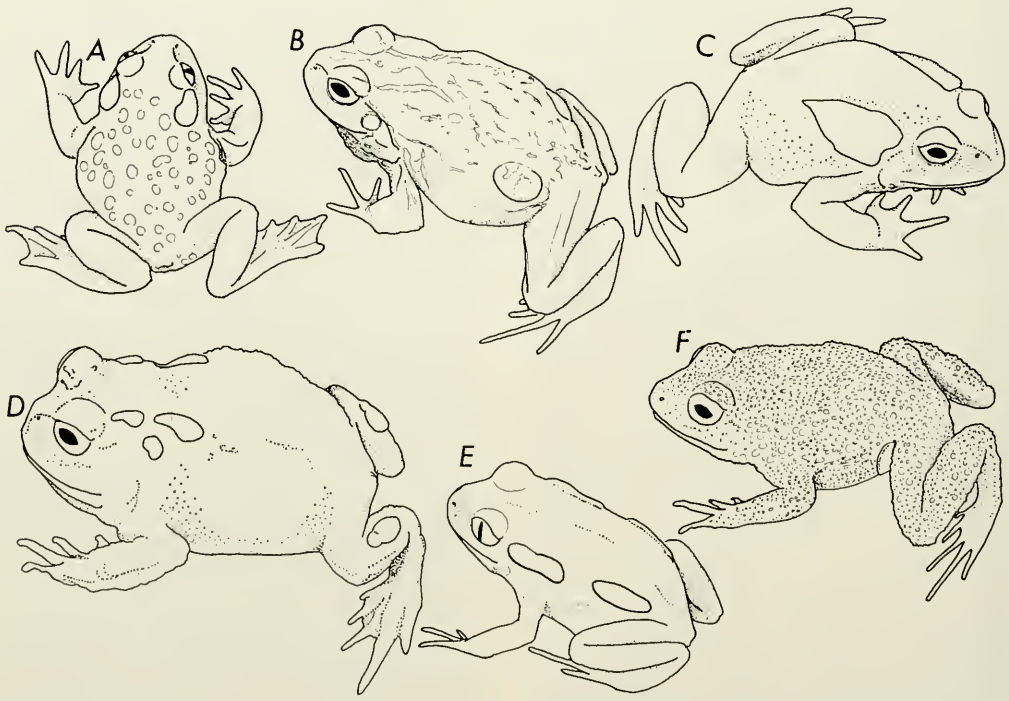

FIGURE 7. Body glands in leptodactylid frogs. (A) *Telmatobufo bullocki,* FMNH 23842, × .5, parotoid glands; (B) *Pleurodema cinera,* KU 80829, × 1, lumbar gland; (C) *Philoria frosti,* KU 110344, × 1, parotoid gland; (D) *Odontophrynus cultripes,* KU 92974, × .7, parotoid and tibial glands; (E) *Uperoleia rugosa,* KU 93589, × 1.2, parotoid and flank glands; and (F) *Cycloramphus asper,* KU 84715, × 1, inguinal gland.

I have not examined the Neotropical genera for these structures, except in the cases of *Crossodactylus* and *Physalaemus*; Baldauf and Tanzer (1965) provided data for *Syrrhophus*. All three genera exhibit the intermaxillary duct pattern seen in cycloranine frogs. Until study of all of the leptodactylid genera is completed, further comment on internal glands and their significance, if any, must be deferred.

Myology

Thigh musculature, jaw musculature, and the musculature of the hyolaryngeal complex have been important characters in the development of our current concepts of the subfamilies and families of leptodactylid and bufonid frogs. Noble (1922) divided the higher frogs into two suborders (Procoela and Diplasiocoela) based on the shape of the centra in the first presacral and sacral vertebrae and on the nature of the distal tendons of the thigh musculature. Although numerous authors pointed out that, at least as far as the muscles were concerned, the division was artificial, the most conclusive evidence against Noble's scheme was reported by Parker (1940), who based his arguments on Australo-Papuan leptodactylids. He demonstrated a procoelan to diplasiocoelan transition in the distal tendons of the thigh musculature; the procoelan condition (ventral position of the distal tendon of the *m. semitendinosus* relative to the *m. gracilis*) was regarded as more generalized by Parker and found to be restricted to the Cycloraninae, whereas the advanced (diplasiocoelan) condition was found only in the Myobatrachinae. Further evidence that Noble's arrangement is artificial is found in the elosiine leptodactylids. *Crossodactylus* has a ranoid pattern of distal thigh tendons, whereas the closely allied genera, *Hylodes* and *Megaelosia*, have the bufonoid pattern. The significance of this variation is discussed in the systematic summary (Elosiinae, p. 164).

Limeses (1964) defined a bufonid and leptodactylid pattern of thigh musculature based on the patterns in *Bufo* and *Leptodactylus* respectively. She demonstrated a continuum of muscle patterns within the Neotropical leptodactylids from the bufonid condition (*Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Proceratophrys cristiceps*) to an "intermediate" condition (*Macrogenioglottus* and *Proceratophrys*, except *P. cristiceps*) to the leptodactylid condition. She regarded the leptodactylid condition as grading from a cycloramphine pattern (most like the bufonid type) through a telmatobiine pattern to the leptodactylid pattern. Limeses' study demonstrated the inadvisability of using the thigh musculature in classifications above the generic level; she felt that the data supported the contention of Reig and his students that the ceratophryines are familially distinct and more closely allied to bufonids.

Limeses (1964) concluded that the thigh muscle complexes of Noble were "progressive" characters and therefore should not be given much weight in defining families or suborders. Griffiths (1959, 1963) pointed out variability in the distal tendons in the dendrobatids (a variability which overlaps the spectrum seen in myobatrachines), but he still attached considerable importance to the character complex because the musculature supported his unique contention that dendrobatids are a subfamily of ranids.

The conclusion of Tihen (1965) and Inger (1967) that in the course of evolution an increase in the complexity of the musculature is to be expected carries much weight in support of the argument that the diplasiocoelan condition is labile as evidenced by its appearance in the Myobatrachinae, Dendrobatidae, and in *Crossodactylus*. I am not of the opinion, in view of the other data available, that the diplasiocoelan condition in the Myobatrachinae suggests ranoid affinities, although it is not inconceivable

that the origin of the arthroleptine ranids might be the Australo-Papuan Myobatrachinae. At present, the arrangements of the thigh muscles in the cycloranine and myobatrachine leptodactylids are regarded as only one additional character in support of Parker's (1940) subfamilial classification.

Griffiths (1959, 1963) used the musculature of the temporal arch as one of the two characters separating leptodactylids and hylids from bufonids. In the former group the *m. depressor mandibulae* is divided into two slips *(pars tympanicus* and *pars scapularis),* whereas in the bufonids the *pars scapularis* is absent. Limeses (1965) investigated the *m. depressor mandibulae* in several of the "ceratophrydids" and compared her data with that for a number of "normal" leptodactylids. I dissected at least one specimen for each leptodactylid genus except *Amblyphrynus* and *Hylorina* in order to examine the state of the *m. depressor mandibulae.* The only taxa with the bufonid type (*pars tympanicus* only) are *Crinia, Eupsophus juninensis, Lepidobatrachus, Philoria,* and *Pseudophryne.* A massive *pars tympanicus* and minute *pars scapularis* are exhibited in several *Eleutherodactylus (biporcatus, bufoniformis, cornutus, galdi, sulcatus), Proceratophrys* (except in *P. cristiceps*), and *Telmatobufo*; the condition seen in *Ceratophrys* and *Macrogenioglottus* is slightly more leptodactylid, but the *pars scapularis* is still small. In *Odontophrynus* and *Proceratophrys cristiceps* both slips are large. In the remaining leptodactylids both muscle slips are present, and the *pars scapularis* is usually larger.

Starrett (1968) studied the jaw musculature in many anurans and distinguished several insertional patterns of the *m. depressor mandibulae.* She considered the condition of this muscle too variable to be used in defining families but useful at lower taxonomic levels when used in combination with the adductor muscles. Based on my study of most of the leptodactylid genera, I consider the *m. depressor mandibulae* to be of questionable value in leptodactylid frog classification. I did not investigate the condition of the adductor muscles in leptodactylids. The reader is referred to Starrett (1968) for a detailed review of anuran jaw musculature.

An associated character is the pathway of the mandibular ramus of the trigeminal nerve through the muscle blocks. Limeses (1965) investigated this character for several of the broad-headed South American leptodactylids and considered it useful in defining her "Ceratophrydidae"—which included only parts of some genera (for example, *Proceratophrys*).

The musculature of the hyolarynx has been successfully used by several authors in systematic studies of frogs. The musculature is discussed with the hyoid (see below).

Hyolaryngeal Apparatus

Trewavas (1933) investigated the hyolarynx in a wide variety of frogs. Among the sixty species he treated were nine leptodactylids. Parker (1940) used the shape of the hyoid plate, condition of the cricoid cartilage ventrally, and the patterns of insertion of the deeper throat muscles on the hyoid plate in separating the two subfamilies of the Australo-Papuan leptodactylids. Griffiths (1959) described the hyolarynx of *Sminthillus.* Among the potentially useful characters in the hyolarynx of leptodactylids are 1) the extent and shape of the alary process of the hyoid plate, 2) branching of the hyale, 3) variation in the postero-lateral process of the hyoid plate, 4) division (ventrally) of the cricoid cartilage, and 5) attachment of the *m. petrohyoideus anterior* and *m. sternohyoideus* on the hyoid plate.

The cricoid is divided ventrally in all genera of the Myobatrachinae but is complete in all other genera of the family. Griffiths (1963) reported the cricoid to be divided ventrally in *Lepto-*

dactylus prognathus, but I have been unable to verify this observation in my specimens. The esophageal process of the cricoid has been used as a systematic tool, but it is apparently of such variability (poorly to well developed) that its use at the generic level is not wise. In ranoids the esophageal process is elongate, as it is in *Heleophryne,* but in most leptodactylids the process is either reduced in size or only of moderate size.

In the Myobatrachinae, the alary processes of the hyoid are broad and wing-like, and the *m. petrohyoideus anterior* inserts on the alary process. The elongate insertion of the *m. sternohyoideus* begins anteriorly on the hyoid plate medial to the alary process and posteriorly moves nearer the midline of the hyoid plate (Fig. 8). In contrast to the condition seen in the myobatrachines, the cycloranines have a narrow stalked alary process and the *m. petrohyoideus anterior* inserts on the posterolateral edge of the hyoid plate. The *m. sternohyoideus* inserts medially on, but at the edge of, the hyoid plate. Anteriorly, its insertion is like that seen in the myobatrachines, but posteriorly the muscles are disposed more laterad. The muscle disposition in *Heleophryne* is exactly like that seen in the Cycloraninae; the only differences in the hyolarynx between the Cycloraninae and *Heleophryne* are the presence of an anterior process on the cornu and the elongate esophageal process in *Heleophryne.*

Among Neotropical leptodactylids, only the *Leptodactylus marmoratus* group, *Physalaemus* (including *Engystomops* and *Eupemphix*), and *Pseudopaludicola* have the myobatrachine pattern of muscle insertions on the hyoid plate. These genera also have the expanded and wing-like alary processes of the hyoid plate as does *Hydrolaetare.* The alary processes are absent in *Ceratophrys, Euparkerella, Holoaden, Lepidobatrachus, Limnomedusa,* and *Sminthillus. Holoaden* and *Pseudopaludicola* lack the posterolateral processes of the hyoid plate. The posterolateral processes of the hyoid plate are large in the Ceratophryinae and *Limnomedusa* (Fig. 9). This enlargement may be a structural compensation for the loss of the alary processes in these genera. Anterior processes of the cornua are lacking in the Australo-Papuan genera and in about one-half of the Neotropical genera. I found anterior processes of the cornua in *Edalorhina, Eleutherodactylus, Euparkerella, Eupsophus, Holoaden, Heleophryne, Hylactophryne, Ischnocnema, Lithodytes, Megaelosia, Niceforonia, Odontophrynus, Proceratophrys, Physalaemus, Sminthillus, Syrrhophus,* and *Tomodactylus.* Specimens were not available of *Amblyphrynus, Batrachyla, Caudiverbera, Crossodactylodes, Hylo-*

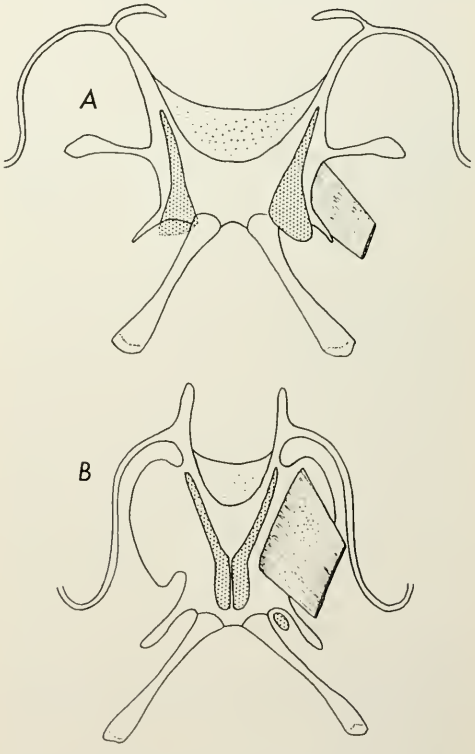

FIGURE 8. Hyoid plates of *Heleophryne natalensis* (A, KU 105925, × 5) and *Physalaemus pustulatus* (B, UIMNH 80710, × 10) illustrating the two muscle insertional patterns. The insertion site for the *m. sternohyoideus* is stippled; the other muscle is the *m. petrohyoideus anterior.*

rina, and *Telmatobufo.* The ceratophryines have broad cornua in comparison to other leptodactylids. The entire hyoid plate is elongate in *Euparkerella, Holoaden,* and *Sminthillus* in contrast to all other leptodactylids (Fig. 9).

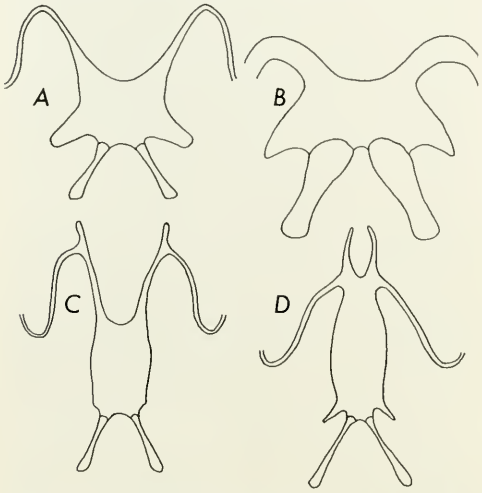

FIGURE 9. Hyoid plates of (A) *Limnomedusa macroglossa* (female, KU 74327, × 2.5), (B) *Lepidobatrachus asper* (male, KU 86782, × 4.5), (C) *Holoden bradei* (female, KU 107086, × 4.5) and (D) *Sminthillus limbatus* (after Griffiths, 1959).

Variations in the hyolarynx appear useful in comparing and contrasting leptodactylid genera. In some cases, the hyolaryngeal data support the classification at the tribe or subfamily level—the Australo-Papuan groups and the Ceratophryinae. The variation in the shape of the hyoid plate among the Neotropical leptodactylids is impressive in view of the uniformity of the structure within the two Australo-Papuan subfamilies.

Chromosome Numbers[3]

In recent years, increasing attention has been given chromosome numbers in Zorrilla and Saez (1968), Morescalchi and Gargiulo (1968), and Morescalchi, Gargiulo, and Olmo (1968). Rabello (1970) summarized much of the data but was unaware of other observations; she published counts contrary to those reported in some of the original work. The somatic counts range from 18 to 104, although Beçak, Denaro, and Beçak (1970) stated that a value of 16 is the lowest known. The highest counts are for polyploid populations. Values of 2N=8X=104 are known for *Ceratophrys dorsata* and *C. ornata* (Barrio and Rinaldi de Chieri, 1970b). Tetraploid counts (2N=4X=44) are known for *Odontophrynus americanus* (Bogart, 1967) and *Pleurodema bibronii* and *P. kriegi* (Barrio and Rinaldi de Chieri, 1970a). The published counts for 67 other *Neotropical* and six Australian leptodactylids range from 18 to 36. The six Australian leptodactylids *(Crinia, Limnodynastes, Pseudophryne,* and *Uperoleia)* have 2N=24 (Morescalchi, Gargiulo, and Olmo, 1968).

The diploid counts for all leptodactylid genera are summerized below. The data are presented as follows: genus (number of species for which counts are known), 2N value(s), and where germane, citations of intrageneric (and intraspecific) variations. Polyploid counts are not repeated here. The names used in the original accounts have been brought into line with the generic classification employed in this work. *Batrachyla* (2), 2N=26; *Caudiverbera* (1), 2N=26; *Ceratophrys* (3), 2N=26; *Crinia* (2), 2N=24; *Crossodactylus* (2), 2N=26, however, Brum-Zorrilla and Saez (1968) reported 2N=22 for *C. gaudichaudii,* whereas Bogart (1970) obtained 2N=26 for the same species; *Cycloramphus* (3), 2N=26, however, Brum-Zorrilla and Saez (1968) reported 2N=22 for *C. fuliginosus (sic.),* whereas Bogart (1970) obtained 2N=26 for the same species; *Eleutherodactylus* (11), 2N=18(2), 20(2), 22(4), 34(2), and 36(1), see Bogart (1970); *Eupsophus* (4), 2N=22(1), 26(1), 28(1), and 30(1), see Bogart (1970) for a detailed account; *Hylactophryne* (1), 2N=22; *Hylodes* (2), 2N=26; *Insuetophrynus* (1), 2N=26; *Lepidobatrachus* (3), 2N=26; *Leptodactylus* (8), 2N=22; *Limnodynastes* (2), 2N= 24; *Lithodytes* (1), 2N=18; *Odontophrynus* (4), 2N=22; *Physalaemus* (6), 2N=22; *Pleurodema* (6), 2N=22; *Proceratophrys* (2), 2N=22; *Pseudopaludicola* (2), 2N=18, 20, and 22, *P. ameghini* is 2N=20 and *P. falcipes* has 2N values of 18, 20, and 22 (Brum-Zorrilla and Saez, 1968, and Batistic, Beçak, and Vizotto, 1969, discussed the situation in this genus); *Pseudophryne* (1), 2N=24; *Syrrhophus* (1), 2N=30; *Telmatobius* (2), 2N=22 and 26, see Barbieri (1954) and Brum-Zorrilla (1968); *Thoropa* (1), 2N=26; *Tomodactylus* (1), 2N=22; *Uperoleia* (1), 2N=24; and *Zachaenus* (1), 2N=26.

James P. Bogart has a considerable amount

[3] The chromosome number account presented here includes only 15 species of leptodactylids. The efforts in this area have greatly increased the number of species (78) for which counts are available. The pertinent literature includes Barrio (1970), Barrio and Rinaldi de Chieri (1970a, 1970b), Beçak (1968), Beçak, Denaro, and Beçak (1970), Bogart (1970), Brum-

systematic studies. Data are only now being accumulated for the leptodactylids, and to date no counts are available for the Australo-Papuan or African genera. Likewise, no data have accumlated for the Neotropical subfamily Elosiinae.

Bogart (1967), Moreschalchi (1967), and Saez and Brum (1959) reported counts for the ceratophryine genera; *Ceratophrys calcarata*, *Chacophrys pierotti*, and *Lepidobatrachus llanensis* have $2n$ of 26, whereas *Ceratophrys ornata* has been reported to have $2n$ of 88, 92, 98, 104, and 108. Bogart (1967) presented convincing arguments that this species is octaploid ($n = 13$).

Of the subfamily Leptodactylinae, counts of $2n$ of 22 are available for five species of *Leptodactylus* and *Pseudopaludicola falcipes* (Barbieri, 1950, Bogart, 1967, and Saez and Brum, 1960).

Counts for the Telmatobiinae range from $2n$ of 22 to 50. The major variation occurs in the genus *Odontophrynus*—*O. americanus* is tetraploid ($2n$ of 44) [Becak, et al., 1966, Bogart, 1967]. Saez and Brum (1966) reported $2n = 42$, 44, and 50 for various populations of this species. The other two species of the genus for which counts are available have $2n$ of 22 (Saez and Brum, 1966). *Telmatobius schreiteri* has a $2n = 26$ (Barbieri, 1954), whereas the other species of the subfamily (except the tetraploid *Odontophrynus americanus*) have $2n = 22$ (*Hylactophryne augusti*, *Tomodactylus nitidus*; Duellman, 1967).

It is generally conceded that the more primitive members of a group have higher chromosome numbers than do the more advanced members of a given group. Although this generalization is supported by too few data to be clearly stated, it is significant that except for the cases of tetraploidy and octaploidy in the leptodactylids, the more primitive Neotropical groups (Ceratophryinae and the Telmatobiini) have diploid numbers of 26, as opposed to 22 in the advanced lines (as determined on other grounds). I anticipate the Cycloraninae and Heleophryninae also to have diploid numbers of 26, as do the pelobatids (Duellman, 1967, Moreschalchi, 1967). The Myobatrachinae might have fewer than 26 since they are morphologically divergent from the Cycloraninae.

OSTEOLOGICAL CHARACTERS

With the notable exceptions of the vertebral centra, sacral diapophyses, terminal phalanges, and the gross pectoral structure, few osteological characters have been used in generic and suprageneric classifications of bufonoid frogs. Cope (1865, 1866, 1889) placed undue weight on minor variations of the skull bones. Subsequent authors, in noting the obvious errors in Cope's scheme, tended to regard most osteological variation as trivial and therefore of no value in a classification at or above the generic level. The most recent author to expound this point was Griffiths (1963). The major efforts in anuran phylogeny have been based on the pectoral architecture (Cope, Boulenger, and Griffiths) and on the vertebral column and thigh musculature (Nicholls and Noble).

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of unpublished observations on leptodactylid chromosome numbers. He has counts for three genera not included above—*Edalorhina* (1), 2N=22; *Heleophryne* (1), 2N=26; and *Ischnocnema* (1), 2N=22—and counts for additional species in eight genera. The additions are *Cycloramphus* (three more species, 2N=26), *Eleutherodactylus* (19 more species, 2N=22 in five, 26 in nine, 30 in three, and 34 in two); *Hylodes* (one more species, 2N=26); *Leptodactylus* (eight more with 2N=22, and two species of the *marmoratus* group, subgenus *Adenomera*, with 2N=26); *Physalaemus* (six more species, 2N=22); *Syrrhophus* (one more species, 2N=26); *Telmatobius* (three more species, 2N=26; one of these is *T. montanus* which Gallardo, 1970, placed in *Alsodes*); and *Thoropa* (one more species, 2N=26). These 47 species increase the total known to 126 representing 29 genera and all seven subfamilies. The subfamilies have counts of: Cycloraninae, 2N=24, Myobatrachinae, 2N=24, Heleophryninae, 2N=26, Ceratophryinae, 2N=26 (and 8X=104), Elosiinae, 2N=26, Leptodactylinae, 2N=18, 20, 22, and 26 (and 4X=44), and Telmatobiinae, 2N=18, 20, 22, 26, 28, 30, 34, and 36 (and 4X=44).

I am convinced that at least within the Bufonoidea, the osteocranium can serve as a primary source of characters for classification. I have completed a generic-level analysis of the skeletons of the frog family Leptodactylidae and have briefly checked certain points among the genera of the Bufonidae, Centrolenidae, Dendrobatidae, Hylidae, and Pseudidae. Additional data are available in the pectoral and pelvic girdles and in the vertebral column. I consider the appendicular skeleton of relatively little use, although the shape of the terminal phalanges and the fusion of the tarsal bones are useful sources of characters.

Maxillary Arch

The premaxillae, maxillae, septomaxillae, and quadratojugals make up the maxillary arch. The quadratojugals are the only bones that are variable in occurrence. In no case are the premaxillae fused. Loss of the quadratojugals occurs sporadically throughout frog families from the most primitive *(Leiopelma, Pipa)* to the advanced (some *Hyla*). The quadratojugals have been lost in six leptodactylid genera—*Batrachyla, Crossodactylus, Hylorina, Notaden, Pleurodema,* and *Pseudopaludicola.* The maxillary arch is incomplete (Fig. 10) but the quadratojugal is present in several leptodactylids. The degree of separation of the maxilla and quadratojugal is variable. Most leptodactylids have the quadratojugals in articular contact with the maxillae, although the contact is tenuous in some genera *(Hylodes).*

Fusion of the elements of the maxillary arch (maxilla and quadratojugal) is seen only in the genera of the subfamily Ceratophryinae *(Ceratophrys* and *Lepidobatrachus).* These frogs and the Chilean *Caudiverbera caudiverbera* have bony, stegocephalian-like skulls with a complete and small orbit. In contrast to the latter genus, the ceratophryines are characterized by the fusion of all of the skull bones (except the columellae, septomaxillae, and premaxillae) into an akinetic unit.

Loss of the maxillary and premaxillary teeth was once considered a family character in frogs, and very often its use resulted in the erroneous association of several leptodactylids with the Bufonidae. In his later works, George A. Boulenger laid an ever decreasing emphasis on the lack of teeth in the maxillary arch. Noble (1922) completely dismissed the character and combined the Bufonidae and Leptodactylidae. Subsequent authors have usually considered loss of the teeth of the maxillary arch of at least generic value; even Noble (1925) later decided that the presence or absence of maxillary teeth was a generic character.

If Moore (1961) is correct in recognizing a single species of *Uperoleia,* then at least one species of frog has intraspecific variation in the presence of teeth on the maxillary arch. Most leptodactylids have teeth on the maxillary arch;

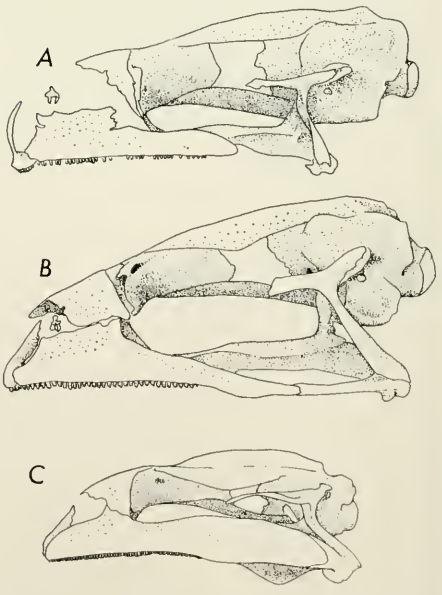

FIGURE 10. Lateral views of the skulls of (A) *Batrachyla leptopus* (UMMZ S-2246, × 6.5), (B) *Eupsophus roseus* (AMNH 22104, × 4.2) and (C) *Cycloramphus eleutherodactylus* (KU 92785, × 3.3) illustrating variation in the extent of the quadratojugal bone.

Batrachophrynus, Glauertia, Metacrinia, Myobatrachus, Notaden, some species of *Physalaemus (maculiventris, nanus, nattereri, obtectus, petersi, pustulosus,* and *signiferus), Pseudophryne, Sminthillus,* some species of *Telmatobius,* and some *Uperoleia* lack teeth. *Phrynanodus nanus* Ahl was long thought to be toothless, but examination of the unique holotype revealed a full complement of teeth and satisfied me that the monotypic genus was identical to *Eleutherodactylus parvus* (Lynch, 1968c).

Loss of teeth is either uniform or variable in ten leptodactylid genera; these genera belong to four clearly definable subfamilies, none of which is defined by tooth loss. *Notaden* is the only cycloranine which has no teeth; it is closely related to *Neobatrachus,* a toothed genus. Of the five toothless myobatrachine genera, *Pseudophryne* is most closely related to *Crinia,* a toothed genus; the other four edentate genera form a group but are not closely related to one another. Tooth loss occurs in the subfamily Leptodactylinae only in *Physalaemus.* Not all species of the genus lack teeth; this variation has contributed to unnatural classifications, in which some species of the genus were placed in the Bufonidae and others in the Cystignathidae. Most of the species of the *nattereri* and *petersi* groups of *Physalaemus* lack teeth—one species in each group has teeth. All species of the *Physalaemus cuvieri* group have teeth. *Batrachophrynus* and its Oligocene relative, *Neoprocoela,* are toothless but closely allied to the toothed genera, *Caudiverbera, Telmatobufo,* and *Telmatobius.* A few species of *Telmatobius* are toothless and have been erroneously associated with *Batrachophrynus.* As Vellard (1951) and Cei and Roig (1968) pointed out, the toothless species of *Telmatobius* are closely related to toothed species. *Sminthillus* is an edentate derivative of the West Indian complex of *Eleutherodactylus.*

Noble (1931) contended that the Criniinae (=Cycloraninae + Myobatrachinae) had deeper maxillae than did the Neotropical leptodactylids. His observations apparently were very limited because among the Australo-Papuan leptodactylids, the Myobatrachinae have shallow maxillae (little or no facial lobe of the maxilla) whereas deep maxillae are found in the Cycloraninae. The maxillae of the cycloranines are no deeper than those seen in many Telmatobiinae (e.g., some *Eleutherodactylus, Odontophrynus, Proceratophrys*) or Leptodactylinae *(Pleurodema).* The depth of the maxilla appears to be correlated with the degree of reduction of ossification. *Uperoleia* and *Myobatrachus* have deeper maxillae than the other myobatrachines, and *Uperoleia* is the only myobatrachine lacking an extensive frontoparietal fontanelle.

The alary processes of the premaxillae are well developed in all leptodactylid genera, except *Myobatrachus,* in which they are essentially obsolete (Fig. 11). The extensive reduction of the anterior portion of the skull of *Myobatrachus* has resulted in minute premaxillae. The palatal shelf is still well developed and similar to those of the other Myobatrachinae. The reduction of the anterior cranial elements in *Myobatrachus* is compensated for by the development of massive palatines.

The alary processes are directed anterodorsally, dorsally, or posterodorsally (Fig. 10), and the slope is apparently correlated with the development of burrowing habits; the more posterior the slope, the greater the burrowing tendencies. In several genera, most notably members of the Elosiinae, the alary processes have a lateral vector as well. In general, the alary processes are relatively narrow near their base in the African and Neotropical genera (Fig. 11), whereas the processes are very broad at the base in the majority of the Australo-Papuan genera (Fig. 11). The range of variation of this character in the sub-

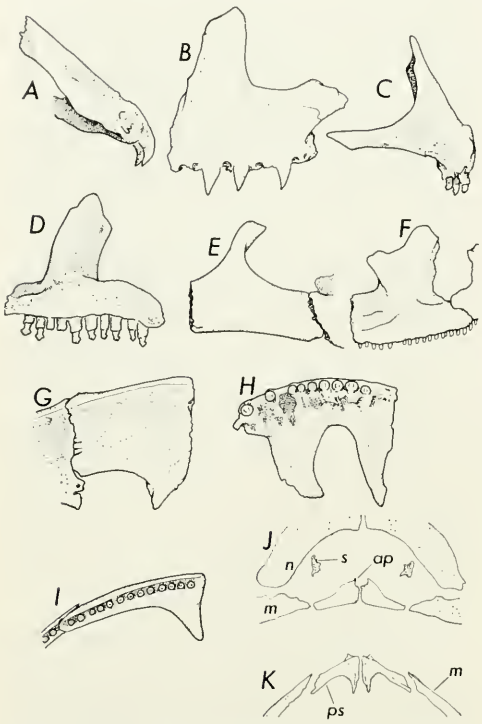

FIGURE 11. Variation in the premaxillae of leptodactylids. (A) median view of left premaxilla of *Ceratophrys calcarata*, JDL S-237, × 2.5; (B) frontal view of same; (C) median view of left premaxilla of *Eleutherodactylus curtipes*, JDL S-351, × 10; (D) frontal view of same; (E) frontal view of left premaxilla of *Batrachophrynus macrostomus*, KU 98127, × 2; (F) frontal view of left premaxilla of *Mixophyes fasciolatus*, KU 56627, × 2.5; (G) ventral view of right premaxilla of *Batrachophrynus macrostomus*, KU 98127, × 2; (H) ventral view of right premaxilla of *Eleutherodactylus curtipes*, JDL S-351, × 10; (I) ventral view of right premaxilla of *Batrachyla leptopus*, UMMZ S-2246, × 9; (J-K) frontal and ventral views of bones of snout of *Myobatrachus gouldi*, KU 110333, × 5. Following abbreviations are used: *m*—maxilla, *n*—nasal, *s*—septomaxilla, *ap*—alary process, and *ps*—palatal shelf.

family Telmatobiinae is as great as the variation throughout the family.

The palatal shelf of the premaxilla is functionally absent in the Ceratophryinae but present in all other leptodactylid genera. The variation in this structure in the non-ceratophryines involves depth of the shelf, degree of medial dissection, and the development of the palatal process (Fig. 11). Deep palatal shelves characterize *Batrachophrynus* and *Neoprocoela* and may reflect loss of teeth, although the shelf is relatively deep in *Holoaden*, a toothed genus. *Batrachyla*, *Crossodactylus*, and *Hylodes* have very shallow palatal shelves and long palatal processes. *Telmatobius* and *Thoropa*, and to a lesser extent, *Physalaemus*, have shallow palatal shelves, which extend laterally to meet the maxillae. In each case, the palatal process is either elongate or large, or both. Deeply dissected palatal shelves occur in *Eleutherodactylus*, *Hylactophryne*, *Ischnocnema*, *Lithodytes*, *Niceforonia*, *Paratelmatobius*, some *Physalaemus*, *Proceratophrys*, *Sminthillus*, *Syrrhophus*, and *Tomodactylus*. The shelf is most deeply dissected in some *Eleutherodactylus*, *Hylactophryne*, *Niceforonia*, and *Tomodactylus*. The depth of the palatal shelf may reflect stress on the anterior end of the skull during burrowing.

The Australo-Papuan genera exhibit almost no variation in the shape and extent of the palatal shelf.

The maxillae show only minor variation in the depth of the facial lobe, the degree of flaring of the maxilla, and the development of exostosis. *Megaelosia* is unique among leptodactylids in its posterior expansion of the maxilla (Fig. 12), which is characteristically a tapering bone. Exostosis is seen in *Caudiverbera*, *Cyclorana australis*, the ceratophryine genera, some *Eleutherodactylus* (*cornutus* and *unistrigatus* groups), and some species of *Proceratophrys*.

The range of variation in the palatal shelf of the maxilla is less than that in the premaxilla. In most genera, the posterior end of the maxillary palatal shelf is expanded (pterygoidal process) and abuts or overlaps the anterior ramus of the pterygoid. In some genera (e.g., *Caudiverbera*), there is a definite suture between the pterygoidal process and the pterygoid (Fig. 12). This character is apparently correlated with a more solid skull architecture.

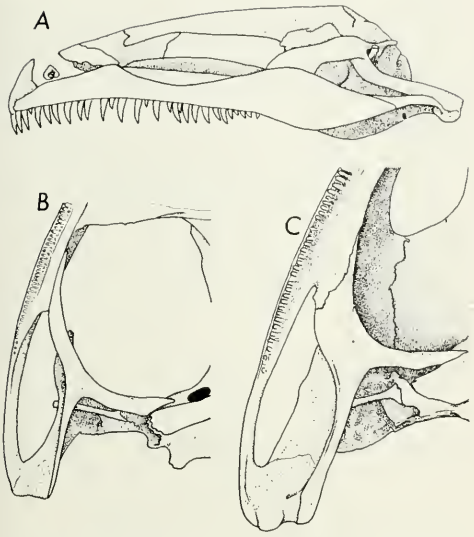

FIGURE 12. Expansion of the posterior portion of the maxilla in (A) *Megaelosia goeldi* (KU 92966, × 4). Maxilla-pterygoid articulation in (B) *Leptodactylus pentadactylus* (KU 68159, × 1) and (C) *Caudiverbera caudiverbera* (FMNH 9703, × 1).

Teeth, when absent on the premaxilla, are also absent on the maxilla. In all toothed genera except *Adelotus*, the teeth form a continuous row from the suture between the premaxillae to a point near the end of the maxilla, posterior to the maxilla-pterygoid junction. In *Adelotus* (Fig. 13) there is a distinct diastema between the maxillary and premaxillary teeth.

Leptodactylid teeth are of two types, exemplified by *Ceratophrys* and *Odontophrynus*. In *Ceratophrys* and four other genera, the teeth are fang-like, some (e.g., *Megaelosia*) more so than others, whereas in *Odontophrynus* and most other genera, the teeth are blunt with some indications of bulbing and cusp formation (like that described for several hylids—Duellman and Trueb, 1966, Trueb, 1966). The teeth in *Megaelosia* are six to seven times as long (proportionately) as those in most other leptodactylids.

Parsons and Williams (1962, 1963) characterized the Lissamphia by numerous features, one of which was jointed or hinged teeth—a basal pedicel and a distal crown. Reig and Limeses (1963) pointed out that the ceratophryine genera do not have hinged teeth, whereas the genera often wrongly combined with *Ceratophrys* [*Odontophrynus* and *Proceratophrys* (=*Stombus auctorum*)] possess hinged teeth. The ceratophryines have comparatively long teeth (here termed "fang-like" for purposes of discussion). Among the American genera, elongate fang-like teeth are found in *Ceratophrys* (including *Chacophrys*), *Lepidobatrachus*, *Megaelosia*, and *Telmatobius*. The teeth of *Crossodactylus*, *Hylodes*, and *Telmatobufo* tend to be pointed and elongate but are not comparable to those of members of the "fang-like teeth" group. Distinct pedicel-crown development is seen in the "fanged" *Megaelosia* and *Telmatobius* but not in the Ceratophryinae (Fig. 13).

Among the toothed Australo-Papuan leptodactylids, fang-like teeth are found only in the cycloranine *Adelotus*; it and all other toothed Australo-Papuan genera and *Heleophryne* have pedicelate teeth.

Goin (1959) published a note on the number of teeth per maxilla in approxi-

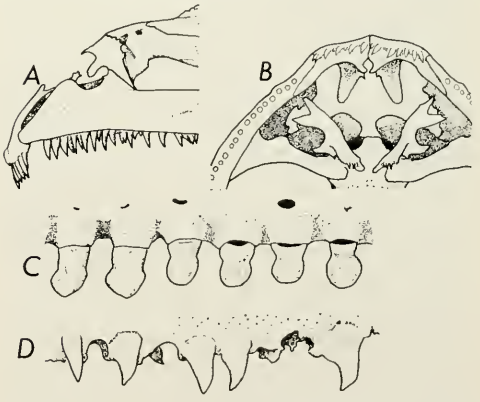

FIGURE 13. (A,B) Anterior portion of the skull of *Adelotus brevis* (KU 56242) illustrating the diastema. (C) Maxillary teeth of *Proceratophrys appendiculata* (KU 93070) and (D) same of *Ceratophrys calcarata* (JDL S-237). Teeth of *Proceratophrys* are pedicellate; those of *Ceratophrys* are non-pedicellate. A and B, × 3; C and D, × 12.5.

mately 65 species of *Eleutherodactylus* and 12 species of *Leptodactylus*; the range in the former was 33 to 111 per maxilla and in the latter 43 to 79. Goin asserted that, within the species groups with which he was familiar, the species groups could be characterized on the basis of average number of teeth. I consider the number of teeth, in most cases, to more accurately reflect the average size of the species studied than relationships. Most species of *Eleutherodactylus* have between 50 and 80 teeth on each maxilla. Reig and Limeses (1963) noted the low tooth counts of the ceratophryines (about 25 per maxilla) as compared with 50 or more per maxilla in most other leptodactylids. They reported the following data for the ceratophryines: *Chacophrys*, 22 ± 2 per maxilla; *Ceratophrys*, 27 ± 3, and *Lepidobatrachus*, 28 ± 5. In *Megaelosia* there are 29 to 34 teeth per maxilla (based on four individuals); these data compare favorably with those for the ceratophryines and for *Adelotus* (26 to 28 teeth per maxilla).

The septomaxillae are small, inconspicuous elements of the maxillary arch and are intricately associated with the nasal cava. The shape of the bones reflects the connecting pathways of the cava. The septomaxillae are proportionately minute in *Ceratophrys* when compared with those of most leptodactylids. The smallest species of the family have simple U-shaped septomaxillae (Baldauf and Tanzer, 1965). I have examined few leptodactylids for the detail of the septomaxillae, but have determined that the bones are invariably present. The septomaxillae of several genera of leptodactylids are illustrated in Figure 14. Serious study of the septomaxillae will probably require study of serially sectioned materials.

Lower Jaw

The anuran mandible contains two bones, the dentary and angular, and the mentomeckelian cartilage (Fig. 15). No leptodactylid has true teeth on the lower jaw, although odontoids are developed to varying degrees by several species. *Grypiscus* was once thought to have mandibular teeth, but Noble (1922) reported these "teeth" to be a serrate ridge. I have not found a serrate ridge on the mandible of any *Cycloramphus (=Grypiscus)* or any other leptodactylid frog except large *Ceratophrys*. Many individuals of *Ceratophrys* have a sharp odontoid on the mentomeckelian cartilage near the mandibular symphasis. The only leptodactylid with large odontoids is *Adelotus brevis* (Fig. 15). These tusk-like odontoids are better developed in the male than in the female. The maxillary diastema of *Adelotus* is apparently a spacing adaptation for the oc-

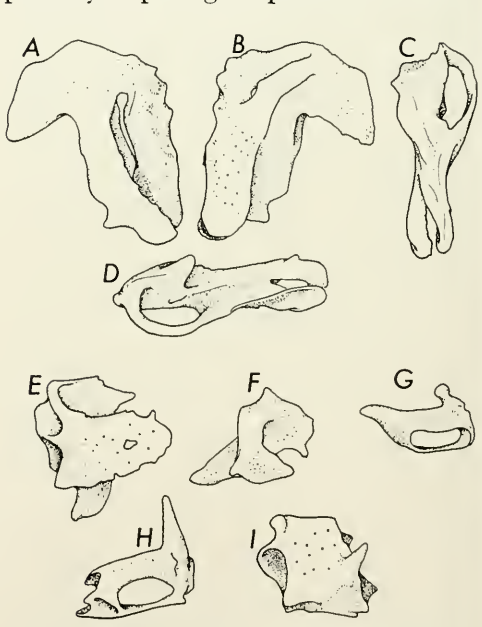

FIGURE 14. Septomaxillae of several Neotropical leptodactylid frogs. (A-D) dorsal, ventral, lateral and median views of right septomaxilla of *Leptodactylus pentadactylus* (KU 84982, × 9.5), (E) ventral view of right septomaxilla of *Eleutherodactylus fleischmanni* (KU 68158, × 9.5), (F) posteroventral view of right septomaxilla of *Ceratophrys calcarata* (JDL S-237, × 16), (G) lateral view of left septomaxilla of *Hylodes lateristrigata* (KU 92878, × 9.5), (H-I) lateral and dorsal views, respectively, of left septomaxilla of *Telmatobius hautholi* (KU 72879, × 9.5).

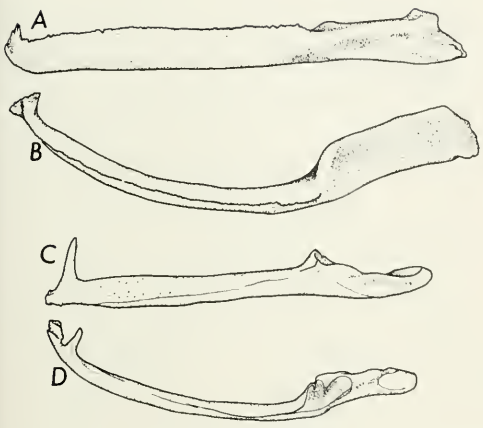

FIGURE 15. Left mandibles of (A-B) *Ceratophrys aurita* (EHT 1415, × 1), and (C-D) *Adelotus brevis* (AMNH 59490, × 2.5). Lateral and dorsal views, respectively.

clusion of the teeth of the maxillary arch and the odontoid of the dentary.

Roof of the Skull

The following bones are included in this category: nasals, sphenethmoid (endochondral), frontoparietals, proötics, and exoccipitals. Unlike some of the casque-headed hylids, the casque-headed leptodactylids always lack a dermal sphenethmoid. Trueb (1966, 1970) reported a dermal sphenethmoid in some casque-headed, co-ossified hylids *(Aparasphenodon, Corythomantis,* some *Hyla, Osteocephalus, Trachycephalus,* and *Triprion petasatus).* The frontoparietals and nasals are co-ossified in *Caudiverbera* and the Ceratophryinae, and are extensively exostosed in *Cyclorana australis* and several *Eleutherodactylus.* Functionally, the proötic and exoccipital form a single bone (otoccipital), although they are not always fused (perhaps paedomorphic).

The nasals exhibit considerable variation in size and position relative to the premaxillae, sphenethmoid, and frontoparietals. Large nasals are present in some members of those genera with the nasals in medial contact (e.g., *Eleutherodactylus*), and small nasals are usually correlated with medial separation (e.g., *Hylodes*). In general, widely separated nasals are correlated with a proportionately large sphenethmoid; however, large sphenethmoids may also be found in genera with closely juxtaposed nasal bones. Separation of the nasals does not always correlate with the presence of a large frontoparietal fontanelle (Fig. 16). A large sphenethmoid usually is correlated with an anterior rotation of the alary processes of the premaxillae, presumably reflecting the forward shift of the nasal capsule. At present, I am unwilling to state that nasal and frontoparietal separation always correlates with a reduction in the amount of bone in the skull or that the enlargement of the sphenethmoid correlates with the above. I consider the variations in the bones of the roof of the skull as discordant. A frontoparietal fontanelle is present in juveniles of all leptodactylids [even *Ceratophrys* just before metamorphosis (Fig. 74)] but is retained in relatively few genera (21) in the adult. The South African *Heleophryne* has a large frontoparietal fontanelle, and large fontanelles are seen in the myobatrachine genera *Crinia, Glauertia, Metacrinia, Myobatrachus,* and *Pseudophryne* but not in *Taudactylus* or *Uperoleia.* The skull roof is solid in the cycloranines *Adelotus, Cyclorana, Lechriodus,* and *Mixophyes,* whereas in *Heleioporus, Kyarranus, Limnodynastes, Neobatrachus, Notaden,* and *Philoria* moderately well-developed frontoparietal fontanelles are present. Frontoparietal fontanelles are lacking in the Ceratophryinae, Elosiinae, and all but two genera of the Leptodactylinae *(Paratelmatobius* and *Pleurodema),* although the leptodactyline *Pseudopaludicola* could be described as having a long, narrow fontanelle (Fig. 17). Among the Telmatobiinae, only two genera *(Batrachyla* and *Thoropa)* have moderate-sized fontanelles; small fontanelles are found in *Batrachophrynus, Eupsophus, Holoaden, Neoprocoela, Telmatobius,* and *Telmatobufo.* The skull is completely roofed in the other

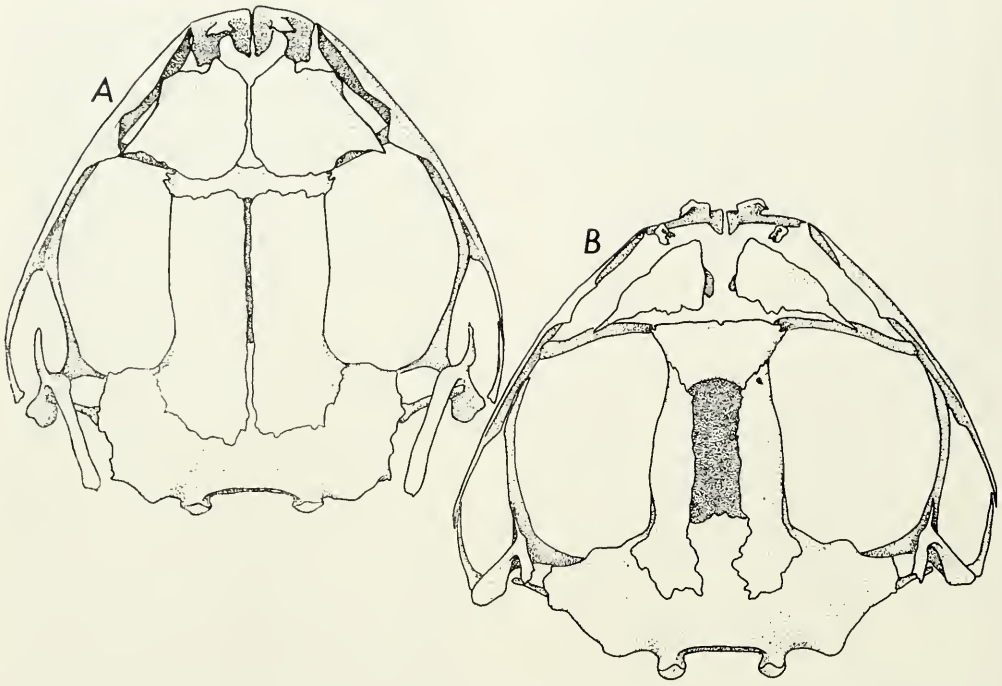

FIGURE 16. (A) Skull of a leptodactylid lacking a frontoparietal fontanelle (*Eleutherodactylus diastema*, KU 68263) and (B) one with a relatively large fontanelle (*Thoropa lutzi*, KU 92850). Both × 6.8.

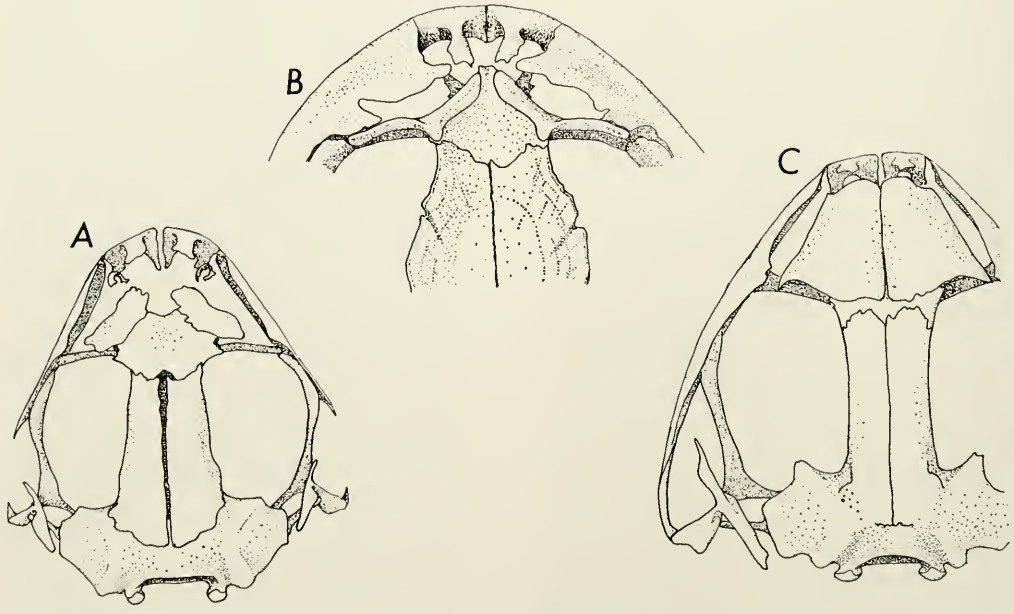

FIGURE 17. Separation of nasal bones. (A) *Pseudopaludicola saltica* (KU 93068, × 6.8); (B) *Proceratophrys boiei* (KU 93076, × 2.3); and (C) *Eleutherodactylus richmondi* (AS 12623, × 4.5).

17 Neotropical leptodactylid genera. Few species of *Eleutherodactylus* characteristically have a frontoparietal fontanelle as an adult. Boulenger (1882) reported this condition in *E. curtipes*, but I think he confused the skeletons of *E. curtipes* and *E. whymperi*.

The nasals are in median contact in *Amblyphrynus, Barycholos, Batrachophrynus, Caudiverbera, Crossodactylodes, Cycloramphus, Eleutherodactylus, Hylactophryne, Ischnocnema, Mixophyes, Philoria, Scythrophrys, Syrrhophus, Tomodactylus, Zachaenus,* in all but two genera *(Paratelmatobius* and *Pseudopaludicola)* of the Leptodactylinae, the Ceratophryinae, and are in contact or very narrowly separated in all but one genus *(Taudactylus)* of the Myobatrachinae. The nasals are slightly to moderately separated in *Adelotus, Cyclorana, Euparkerella, Eupsophus, Heleioporus, Holoaden, Hylorina, Limnodynastes, Megaelosia, Neobatrachus, Niceforonia, Notaden, Odontophrynus, Paratelmatobius, Proceratophrys, Sminthillus, Telmatobius, Telmatobufo,* and *Thoropa*. The nasals are widely separated in *Batrachyla, Crossodactylus, Heleophryne, Hylodes, Kyarranus, Pseudopaludicola* and *Taudactylus*. In those genera with slight separation of the nasals, the separation may be due to a general reduction of bone or to an anterior extension of the sphenethmoid, as in *Proceratophrys* (Fig. 17). Without developmental studies, separation of the latter two groups is not feasible.

Contact between the nasals and frontoparietals is uncommon in the Leptodactylidae. When these bones are in contact, the sphenethmoid is not visible dorsally unless there is a partial separation of the frontoparietals anteriorly (as in *Cycloramphus*) or a posteromedial separation of the nasals (as in *Amblyphrynus, Eleutherodactylus,* and *Proceratophrys*). Relatively broad nasal and frontoparietal contact occurs in the genera *Caudiverbera, Ceratophrys, Cycloramphus, Hydrolaetare, Lepidobatrachus,* and *Philoria;* tenuous contact occurs in *Glauertia, Mixophyes,* and *Myobatrachus*. The nasals and frontoparietals of all specimens of *Leptodactylus* I have examined are separated, although Gallardo (1964) reported contact in the *Leptodactylus ocellatus* group.

Ornamentation of the frontoparietals, as expressed externally in cranial ridges or crests, has been noted by many authors dealing with the Leptodactylidae. Development of crests has often influenced generic recogniton (e.g., *Eleutherodactylus biporcatus, cornutus,* and *galdi* groups). Much of the early systematic study of the Bufonidae involved minor variations in the development of such crests, and it is in *Bufo* that the greatest development of crests occurs (e.g., *Bufo typhonius*). The frontoparietal ornamentation in leptodactylids varies from slight ridges above the orbits *(Niceforonia)* to the heavy crest development and exostosis seen in *Cyclorana australis, Eleutherodactylus biporcatus, E. cornutus, E. devillei, E. galdi, E. sulcatus,* and *Proceratophrys cristiceps,* to the dermostosis of the skull bones seen in the ceratophryines and *Caudiverbera*. The ornamentation begins at the lateral edges of the frontoparietals near the posterior edge of the orbit and proceeds posteriorly, then medially, and finally anteriorly. Concurrent with the development of ornamentation on the nasals, ornamentation begins on the otic plate of the squamosal.

The thickening of the frontoparietal posteriorly and/or the involvement of the dermis of the head in co-ossification results in the enclosure of the carotid artery in a bony canal. Posteriorly, this results in a carotid foramen (Figs. 18-19). Distinct carotid foramina are found in the ceratophryines and *Caudiverbera,* but not in other Neotropical genera. The carotid artery usually passes above the otic region of the skull between the epiotic eminences and the edge of the frontoparietal shelf. This is true of *Heleophryne* and all Australo-Papuan genera

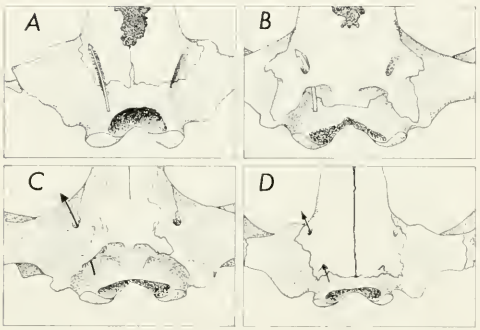

FIGURE 18. Occipital canal and foramen development in non-casque-headed leptodactylids. (A) open canal, *Notaden nichollsi*, KU 93582, × 1.2, (B) short enclosed canal, *Heleioporus eyeri*, UMMZ 124504, × 1.4, (C) long enclosed canal, *Mixophyes fasciolatus*, KU 56627, × 1.2, and (D) *Lechriodus fletcheri*, AMNH 59488, × 1.4.

except *Cyclorana, Heleioporus, Kyarranus, Lechriodus, Mixophyes, Neobatrachus, Notaden,* and *Philoria.* In *Cyclorana* and *Notaden* the carotid artery lies in a shallow or deep, exposed channel (Fig. 18), whereas in the other genera the passage is overlain by bone to form a short *(Heleioporus, Kyarranus, Neobatrachus,* and *Philoria)* to long *(Lechriodus* and *Mixophyes)* canal (Fig. 18).

The crista parotica is, for purposes of my discussion, more a region than a

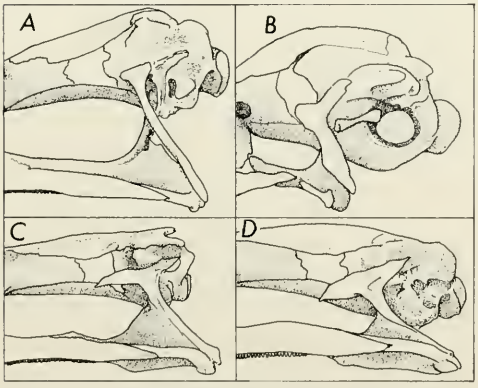

FIGURE 19. Squamosal-maxillary angles in leptodactylid frogs. (A) *Neobatrachus pictus,* ∠ =55° (FMNH 97281, × 1.2, (B) *Myobatrachus gouldi,* angle not subject to measurement (KU 110333, × 2.4, (C) *Eleutherodactylus bufoniformis,* ∠ =53° (KU 80621, × 0.6), and (D) *Leptodactylus insularum,* ∠ =36° (KU 41026, × 0.6).

structure. It is the otoccipital (fused proötic and exoccipital) lateral to the epiotic eminences. In leptodactylids the cristae paroticae are either short and stocky or long and narrow. In *Eleutherodactylus* these two groups tend to grade into one another.

Fusion of the otoccipital to the frontoparietal is known in several bufonid groups (Tihen, 1960a, 1962a) as well as in *Syrrhophus* (Baldauf and Tanzer, 1965). Among the 57 genera of leptodactylids this fusion occurs only in *Eleutherodactylus* and some of its allies *(Euparkerella, Sminthillus, Syrrhophus,* and *Tomodactylus).* All but one species group of West Indian *Eleutherodactylus* (*inoptatus* group) have the otoccipital and frontoparietal fused, as do some of the species of *Eleutherodactylus* living in the higher parts of the Andes in Colombia, Ecuador, and Venezuela.

Schaeffer (1949) regarded the presence of a temporal arcade (articulation between the squamosal and frontoparietal over the cristae paroticae) to be unique to *Caudiverbera,* among leptodactylids. The distribution of the character in other frog families is sporadic. In several genera, lateral growth of the frontoparietal is such that the frontoparietal almost meets the squamosal, but fails to do so because the squamosal is not expanded medially (*Anotheca, Eopelobates,* and *Pelobates,* except *P. cultripes,* where contact occurs). Several bufonids have a suture between the otic plate of the squamosal and the frontoparietal, as do the following hylid genera: *Aparasphenodon, Corythomantis, Hemiphractus, Pternohyla (fodiens,* but not *dentata), Trachycephalus,* and *Triprion.* The suture is present in only three leptodactylid genera—*Caudiverbera* (including *Eophractus* and *Gigantobatrachus*), *Ceratophrys* (including *Chacophrys*), and *Lepidobatrachus;* these genera include only a dozen species, slightly fewer than the number of species of hylids exhibiting sutural contact between the squamosal and fronto-

parietal. The intrageneric variation in this character in *Pelobates* and *Pternohyla* serves as adequate warning as to the amount of weight that can be given this character; fortuitously, there is no intrageneric variation in this character in the leptodactylid genera, so they can be diagnosed by the presence of the suture. Expression of the sutural contact always accompanies casque development.

Temporal Architecture

Griffiths (1954) pointed out the possible use of the squamosal-maxillary angle in ascertaining the relationships of higher frogs. The squamosal-maxillary angle is the angle formed by the body of the ventral ramus of the squamosal and the maxillary arch. The musculature of the region (principally the *m. depressor mandibulae*) has been used to separate the Pelobatidae from the higher frogs and to separate the Bufonidae (and Atelopodidae) from the Hylidae and Leptodactylidae (see page 34). The discussion here is concerned with the squamosal bone and the associated angle. Griffiths (1954, 1959, 1963) reported that all leptodactylids have squamosal-maxillary angles between 45° and 50° and that the bufonid-atelopodid complex has an angle greater than 55°. My investigation of this character complex does not support Griffiths' statements. Leptodactylids have an observed range of from 15° to nearly 90°. The curvature of the posterior portion of the maxillary arch and the inner edge of the ventral ramus of the squamosal often renders measurements of angles difficult or impossible. In addition to a dorsoventral curvature of the maxillary arch, there is a lateral curvature of the quadratojugal in many genera. Loss of the quadratojugal precludes measurements of the squamosal-maxillary angle. The peculiar rotation of the cranial elements of *Myobatrachus* has resulted in a tenuous contact between the strongly curved (dorso-ventral) quadratojugal and maxilla (Fig. 19). Use of the squamosal-maxillary angle in any suprageneric classification of frogs is hazardous at best. Starrett (1968) came to this same conclusion.

The presence of an otic plate of the squamosal in casque-headed frogs was noted above. In general, the otic element of the squamosal is not well developed and does not overlie the otoccipital. In *Caudiverbera, Ceratophrys,* and *Lepidobatrachus,* the otic plate is large. In *Ceratophrys* a posttemporal fenestra (Fig. 20) is formed by the contact of the squamosal and frontoparietal. The otic plate of the squamosal and laterally expanded frontoparietal rest flush on the otoccipital in *Caudiverbera* and *Lepidobatrachus.*

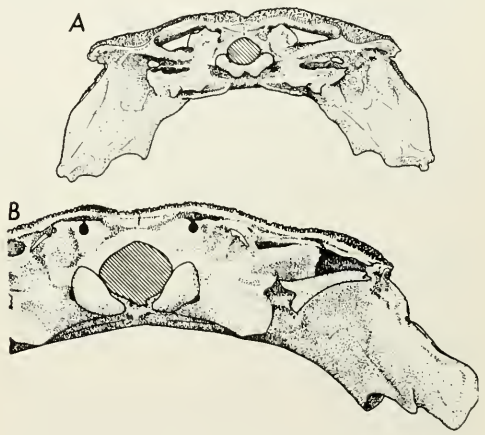

FIGURE 20. Posterior views of skulls of (A) *Ceratophrys calcarata* (JDL S-237) and (B) *Caudiverbera caudiverbera* (FMNH 9703) illustrating presence and absence, respectively, of temporal fenestrae. The lower figure is also a type II occipital condyle arrangement; compare with figure 29B. × 0.5.

In lateral profile, several variations on the "typical" squamosal are apparent in the lengths and sizes of the zygomatic and otic rami (Fig. 21). The myobatrachine genera have short, knob-like zygomatic rami and elongate otic rami of the squamosals. The otic plate, if present, is a narrow structure and not clearly defined. This pattern also occurs in the West Indian *Eleutherodactylus, Smin-*

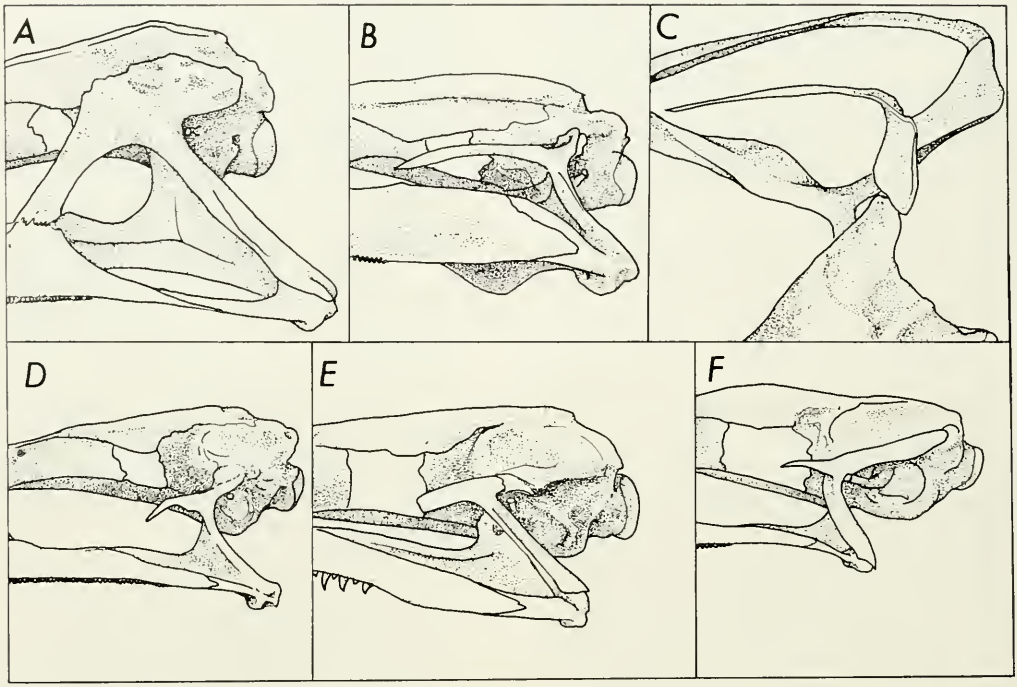

FIGURE 21. Variation in length of rami of squamosals. (A) *Proceratophrys boiei* (KU 93076, × 4), (B) *Cycloramphus eleutherodactylus* (KU 92785, × 3.5), (C) *Zachaenus stejnegeri* (KU 92747, dorsal view × 9), (D) *Eleutherodactylus fitzingeri* (KU 117358, × 3.5), (F) *Telmatobius marmoratus* (UMMZ 68179, × 3), and (F) *Eleutherodactylus diastema* (KU 68263, × 6.8).

thillus, Syrrhophus, Tomodactylus, and a few mainland *Eleutherodactylus.* The otic ramus is very short in *Batrachophrynus, Neoprocoela, Telmatobius,* and *Telmatobufo*; in these genera, the zygomatic ramus is moderate in length. The zygomatic and otic rami of all other leptodactylids (except *Caudiverbera, Ceratophrys, Cyclorana australis, Eleutherodactylus ruthae, Lepidobatrachus, Megaelosia,* and *Proceratophrys)* are equally developed. An otic plate is developed in many groups. *Caudiverbera, Ceratophrys,* and *Lepidobatrachus* have a broad maxillary-squamosal articulation which completes the ventroposterior margin of the orbit. *Cyclorana australis* and *Proceratophrys* have broad articulations between the squamosal and maxilla, but in these species there is no posterodorsal growth of a squamosal process of the maxilla. In *Megaelosia,* there is a strong, ligamentous contact between the bones, but a suture is not apparent. The zygomatic ramus of *Eleutherodactylus ruthae* is very long and in tenuous contact with the maxilla. A similar development of the squamosal was noted in *Cyclorana alboguttata* by Parker (1940).

Determination of the extent of the maxilla and squamosal in the maxillary-squamosal bridge of the ceratophryines is impossible without the aid of a developmental series. Some authors have figured what I consider to be fictitious suture lines. In *Ceratophrys ornata* froglets (stage 46), development of the bridge is clearly evident. The ventral portion of the arch is provided by a posterodorsal growth of the maxilla and the dorsal portion is made up of the zygomatic ramus of the squamosal (Fig. 74).

Palate

Parker (1940) presented a complete survey of the anterior palate in the Australo-Papuan leptodactylids as then

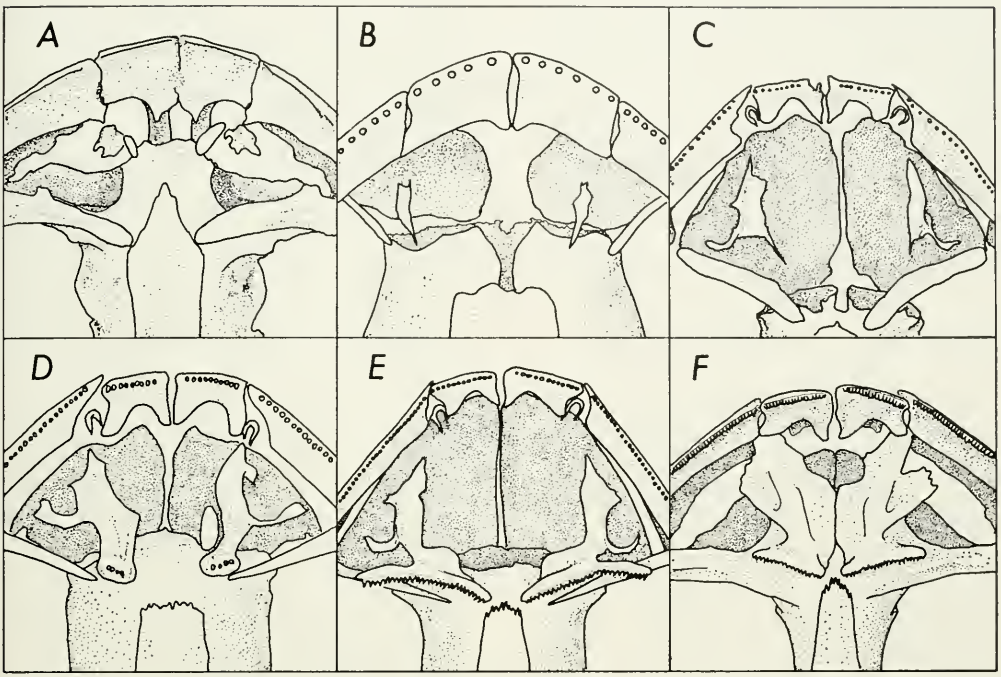

FIGURE 22. Variation in the size of the prevomerine bones of Neotropical leptodactylids. (A) *Batrachophrynus macrostomus* (KU 98127, × 1.2), (B) *Euparkerella brasiliensis* (KU 93192, × 13.4), (C) *Syrrhophus pipilans nebulosus* (KU 59950, × 6.8), (D) *Eleutherodactylus cochrane* (AS V8014, × 9), (D) *E. atkinsi* (AS V6263, ×9), and (F) *E. bufoniformis* (KU 80621, × 2.4).

understood (*Neobatrachus, Philoria,* and *Taudactylus* were not available or not recognized by Parker). Almost no data have been presented on the palate of African or Neotropical leptodactylids except for the papers of Méhely (1904) and Parker (1927) concerning the paludicoline leptodactylids *(Physalaemus, Pleurodema,* and *Pseudopaludicola).*

Primitively, the prevomers are large and toothed; their reduction or loss is a derived condition. The prevomers are minute or absent in all members of the Australo-Papuan Myobatrachinae and the Neotropical genera *Batrachophrynus* and *Euparkerella* as well as in some species of *Eupsophus, Niceforonia,* and *Syrrhophus.* An almost complete, graded series in the size of the prevomers (from large to minute) can be demonstrated within the subfamily Telmatobiinae (Fig. 22). The prevomers are minute in *Batrachophrynus* and are progressively larger in *Euparkerella, Syrrhophus pipilans, Smintillus limbatus, Syrrhophus longipes* (often toothed), *Eleutherodactylus cochranae, E. atkinsi,* and *E. bufoniformis.*

Reduction in the size of the prevomer does not necessarily mean that the prevomerine teeth are lost. Although loss of the prevomer appears to be the trend in *Crinia* and *Syrrhophus,* some members of each genus have prevomerine teeth. The prevomerine teeth have been lost in the following leptodactylid genera: *Batrachophrynus, Crinia* (part), *Crossodactylus, Crossodactylodes, Eleutherodactylus* (part), *Euparkerella, Eupsophus* (part), *Glauertia, Metacrinia, Myobatrachus, Niceforonia* (part), *Physalaemus* (occasionally present in one species), *Pseudopaludicola, Pseudophryne, Smintillus, Syrrhophus* (part), *Taudactylus, Telmatobius* (part, intraspecifically variable), and *Uperoleia.* Only nine leptodactylid genera are completely edentulous *(Batrachophrynus, Glauertia,*

Metacrinia, Myobatrachus, seven species of *Physalaemus, Pseudophryne, Sminthillus, Taudactylus,* and one species of *Uperoleia).*

Loss of the prevomerine teeth has occurred in all members of three other bufonoid families (Bufonidae, Dendrobatidae, and Rhinodermatidae) and occurs sporadically in the Hylidae. In the Dendrobatidae, the prevomerine bones are reduced in size and may be lost in some groups (Fig. 23).

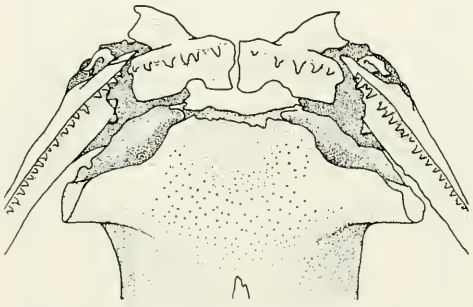

FIGURE 23. Anterior palatal region of *Colostethus panamensis* (KU 77681, × 10).

The telmatobiine genera (Eleutherodactylini) *Eleutherodactylus, Euparkerella, Sminthillus, Syrrhophus,* and *Tomodactylus* show interesting geographic variation in the size and median separation of the prevomers. The prevomers are relatively small and widely separated in the West Indian *Eleutherodactylus, Euparkerella, Sminthillus, Syrrhophus,* and *Tomodactylus,* whereas the bones are relatively larger and only slightly separated or in median contact in the Middle and South American species of *Eleutherodactylus.* Large prevomers (in median contact) are found in the South American genera *Amblyphrynus* and *Ischnocnema*; these genera are probably derivatives of *Eleutherodactylus.*

The prevomers of the Cycloraninae and Heleophryninae are large and toothed. The median separation of the bones varies from moderate *(Notaden)* to none *(Mixophyes).* I recognize two tribes of the Cycloraninae—Cycloranini and Limnodynastini. They differ in breeding biology and in the relative positions of the prevomerine dentigerous processes to the choanae. The dentigerous processes in the Cycloranini lie between the choanae, anterior to the posterior edge of the choanae, whereas in the Limnodynastini, the dentigerous processes lie posterior to the choanae. The dentigerous processes lie anterior to the choanae in *Heleophryne*—the prevomers of this genus are unique (Fig. 73).

Contrary to older reports in the literature, the anuran palatine does not bear teeth. The "palatine teeth" are either odontoids on the palatal bones or are the prevomerine teeth. The palatine bones are present in all leptodactylids, but they are very small in *Crinia, Euparkerella,* and *Pseudophryne.* In *Myobatrachus* the palatines form the major supportive elements of the anterior part of the skull. Palatal ridges occur in several of the larger *Eleutherodactylus,* in *Batrachophrynus, Caudiverbera, Ceratophrys, Proceratophrys,* and in *Cyclorana australis.* Discrete odontoids occur on the palatal ridges in large specimens of *Caudiverbera* and *Ceratophrys.* The palatines are absent in several bufonid genera (Tihen, 1960a) and in all dendrobatids and rhinodermatids. In the dendrobatids, loss of the palatines is compensated for by the development of a large palatal shelf from the posteroventrolateral edge of the sphenethmoid. The dendrobatids are clearly derived from the Elosiinae; in the Elosiinae the palatine bones are present, and a posteroventrolateral palatal shelf develops in *Hylodes* but is not especially evident in the other genera.

The parasphenoid is an unpaired bone covering much of the ventral surface of the skull. It is tri-radiate, with an anterior ramus and two lateral alae. The anterior ramus rests anteriorly on the sphenethmoid, and the alae rest on the otic capsules. In *Batrachophrynus,* the anterior ramus extends well anterior to the palatines—the parasphenoid does not extend farther anterior in any other leptodactylid genus. In the Elosiinae,

the anterior ramus is very short (as it is in dendrobatids). A median keel is found on the parasphenoid in a few leptodactylids—the significance of a median keel is not apparent.

The lateral alae are short or long, oriented at right angles to the anterior ramus or deflected posterior, and overlapped or not by the median rami of the pterygoids (Fig. 24). The alae are overlapped by the median rami of the pterygoids in the Ceratophryinae, Cycloraninae, Heleophryninae, in *Megaelosia,* in *Hydrolaetare, Leptodactylus* (*fuscus, melanonotus, ocellatus,* and *pentadactylus* groups), *Limnomedusa,* and *Pleurodema* (Leptodactylinae), in *Amblyphrynus, Batrachophrynus, Caudiverbera, Crossodactylodes, Cycloramphus, Eupsophus, Hylactophryne, Hylorina, Ischnocnema, Odontophrynus, Proceratophrys, Thoropa,* and *Zachaenus* (Telmatobiinae). In many species of *Eleutherodactylus,* the pterygoid and parasphenoid overlap. The bones are in tenuous contact in *Edalorhina, Hylodes, Physalaemus,* and *Pseudopaludicola,* as well as in some *Eleutherodactylus.* The bones are widely separated in the Myobatrachinae, *Barycholos, Batrachyla, Crossodactylus,* some *Eleutherodactylus, Euparkerella, Holoaden,* some *Leptodactylus* (*marmoratus* group), *Lithodytes, Niceforonia, Paratelmatobius, Sminthillus, Syrrhophus, Telmatobius, Telmatobufo,* and *Tomodactylus.*

Non-overlap of the pterygoid and parasphenoid seems to have been accomplished in two ways—by simple shortening of both elements, or by bending of the median ramus of the pterygoid. The latter means is apparently the most common in the Leptodactylinae, in which an almost complete graded series can be demonstrated.

The tri-radiate, paired pterygoids articulate laterally at two points on the maxillary arch and medially they may (or may not) rest on the otic capsule. The anterior ramus is always longer than the median or posterolateral rami and is either in ligamentous or sutural contact with the maxilla (Fig. 12). Tihen (1962b) used the long anterior ramus of *Neoprocoela* (reaching the palatines) as one character to synonymize the genus with the *Bufo calamita* group. Palatal-pterygoid contact occurs in five telmatobiine genera (*Batrachophrynus, Odontophrynus, Proceratophrys, Telmatobius,* and *Telmatobufo*), one elosiine genus (*Hylodes*), and two leptodactyline genera (*Pleurodema* and *Pseudopaludicola*). The palatines and pterygoids are narrowly separated in the telmatobiine genera *Batrachyla, Eupsophus,* and *Hylorina,* the elosiine genus *Crossodactylus,* and the leptodactyline genera *Limno-*

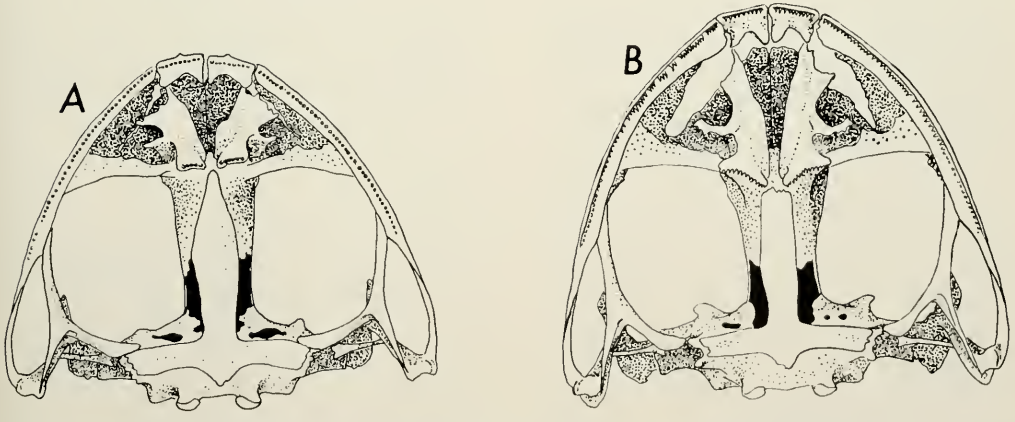

FIGURE 24. Ventral views of the skulls of leptodactylids with a pterygoid-parasphenoid overlap (A) *Eleutherodactylus fleischmanni,* KU 68157, × 2, and one without an overlap (B) *E. inoptatus,* AS X2356, × 2.4.

medusa and *Physalaemus*; these bones are moderately separated in the leptodactyline genera *Edalorhina* and *Lithodytes*. The palatines and pterygoids are narrowly separated in all cycloranines except *Philoria* (wide separation). Actual contact of the bones occurs as a variation in *Adelotus, Cyclorana australis, Heleioporus,* and *Neobatrachus*. They are widely separated in all other leptodactylid genera.

A ventral flange occurs on the body of the pterygoid (Fig. 25) in a few Neotropical genera—*Cycloramphus, Hydrolaetare,* and *Zachaenus*. Principally because of the absence of this character, *Zachaenus roseus* Cope was removed from the genus *Zachaenus*. The holotype of Z. *roseus* is a macerated heap of fragments, and its systematic status is uncertain. The flange may have developed for the attachment of muscles used in burrowing in the genera *Cycloramphus* and *Zachaenus*; *Hydrolaetare* is apparently aquatic, and the flange may reflect the habit of burrowing in mud.

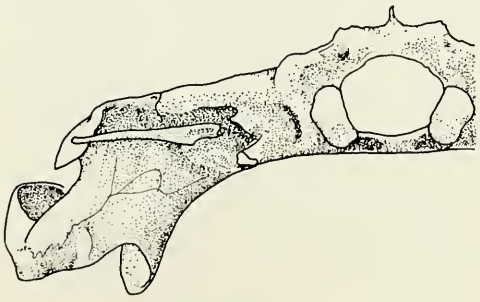

FIGURE 25. Occipital view of the skull of *Cycloramphus dubius* (KU 92780, × 7.5) illustrating the enlarged pterygoidal flange.

Otoccipital and Columella

The otoccipital bone is the fused proötic and exoccipital. These bones are occasionally separate—usually in juveniles and in species with many paedomorphic features. Dorsomedially, the otoccipitals are bordered by the frontoparietals. The frontoparietals and otoccipitals are fused in a few genera of the Eleutherodactylini. Ventrally, the otoccipitals rest on the parasphenoid. The columella is associated with the otoccipital and rests on the cartilaginous operculum. The shape, size, and direction of the columella show some variation; I have not investigated these variations.

The columellae are lacking in *Crossodactylodes pintoi, Euparkerella brasiliensis, Eupsophus juninensis, E. monticola, Holoaden, Paratelmatobius,* all species of *Pseudophryne, Telmatobius niger, Telmatobufo bullocki,* and probably in *Niceforonia simonsii*. I am not willing, at present, to recognize loss of the columella (or entire middle ear) as being of taxonomic value at the generic level.

Gallardo (1965) regarded the degree of median separation of the occipital condyles of considerable importance in discerning intrafamilial relationships of the Leptodactylidae. This character is also reflected in the positions of the atlantal cotyles. Tihen (1962a) cited the form of the occipital condyles as evidence of a close relationship between bufonids and the ceratophryine genera. An essentially heterocoelus condition obtains in *Ceratophrys, Caudiverbera,* and *Lepidobatrachus*—the condyles are not discrete elements. In the Cycloraninae, *Batrachophrynus, Eupsophus, Hylorina, Heleophryne, Limnomedusa, Megaelosia, Pleurodema, Proceratophrys, Telmatobius,* and *Telmatobufo,* the occipital condyles are closely juxtaposed but discrete elements (Fig. 26). In the other 34 Recent leptodactylid genera, the condyles are widely separated. The distinction between "closely juxtaposed" and "widely separated" occipital condyles may be partially size-dependent. The small species of *Leptodactylus* have widely separated condyles whereas the larger species (*pentadactylus* group) have the condyles less widely separated (Fig. 27). The occipital condyles are widely separated in the largest species of *Eleutherodactylus* and in the large-headed *Amblyphrynus*. These observations suggest that some taxonomic

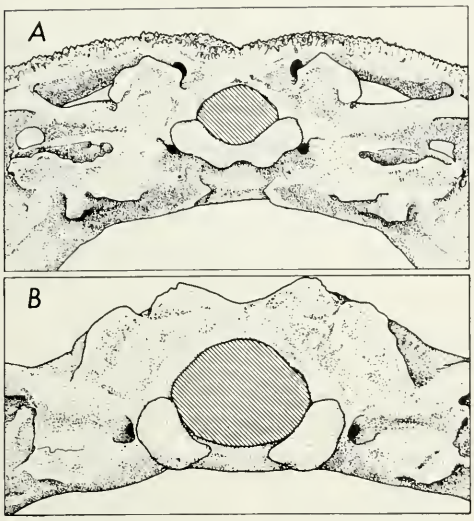

FIGURE 26. Occipital views of skulls of (A) *Ceratophrys calcarata* (JDL S-237, × 2) and (B) *Cycloramia australis* (KU 93550, × 4) showing confluent occipital condyles as opposed to the condylar arrangement typical of a type II cervical cotylar arrangement.

weight may be accorded this character. In small leptodactylid frogs, both conditions are found; I regard this observation as additional evidence in support of the use of this character as a primary tool in systematics of leptodactylids and other bufonid frogs.

The condyles are closely juxtaposed in the primitive frog families, several leptodactylid genera, *Rhinoderma*, and all bufonids. The condyles are widely separated in all other frogs.

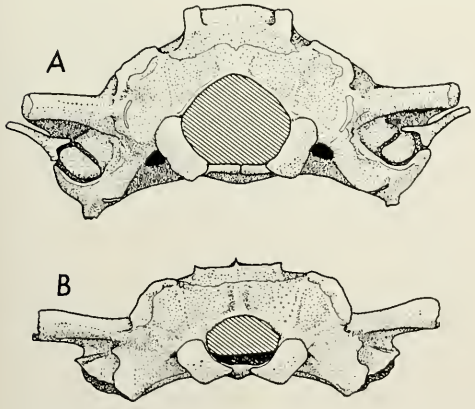

FIGURE 27. Posterior views of skulls of a small *Leptodactylus* (A) *L. quadrivittatus*, KU 41030, × 4, with widely separated occipital condyles and, a large species, (B) *L. pentadactylus*, KU 68159, × 1, with comparatively narrowly separated occipital condyles.

Vertebral Column

All leptodactylids have eight presacral vertebrae, although the first (cervical) and second vertebrae are fused in several genera. In no case is there vertebral deletion of presacral vertebrae (through incorporation into the sacrum) as is known in several bufonids (Noble, 1926b, Tihen, 1960a, 1965). The vertebrae are procoelus in most leptodactylids, but the majority of the Australo-Papuan and African genera have free intervertebral discs (ectochordy) or an unconsolidated intervertebral tissue (a paedomorphic trait). The anuran centrum has been the focus of several lengthy discussions (see Griffiths, 1963, for a summary, and Inger, 1967) and was one of the primary characters that Noble (1922) used in constructing his anuran phylogeny.

Cervical vertebra.—The cervical and first thoracic vertebrae are fused in *Adelotus, Heleioporus, Heleophryne, Kyarranus, Limnodynastes, Neobatrachus, Notaden,* and *Philoria.* The vertebrae are sometimes fused in large specimens of *Ceratophrys* and *Lepidobatrachus,* but in these genera the fusion is variable and most often reflects senility.

As noted above, the occipital condyles are either widely separated or closely juxtaposed. The articular surfaces are either separated or confluent. In those frogs with closely juxtaposed occipital condyles, it is difficult to determine whether the articular surfaces are narrowly separated or confluent; this distinction can be made by examining the cotylar arrangement of the cervical vertebra.

The variation in cervical cotylar arrangements permits the definition of three classes (Fig. 28).

Type I: the cervical cotyles are widely spaced (this class is the concave atlas pattern of Gallardo, 1961, 1965).

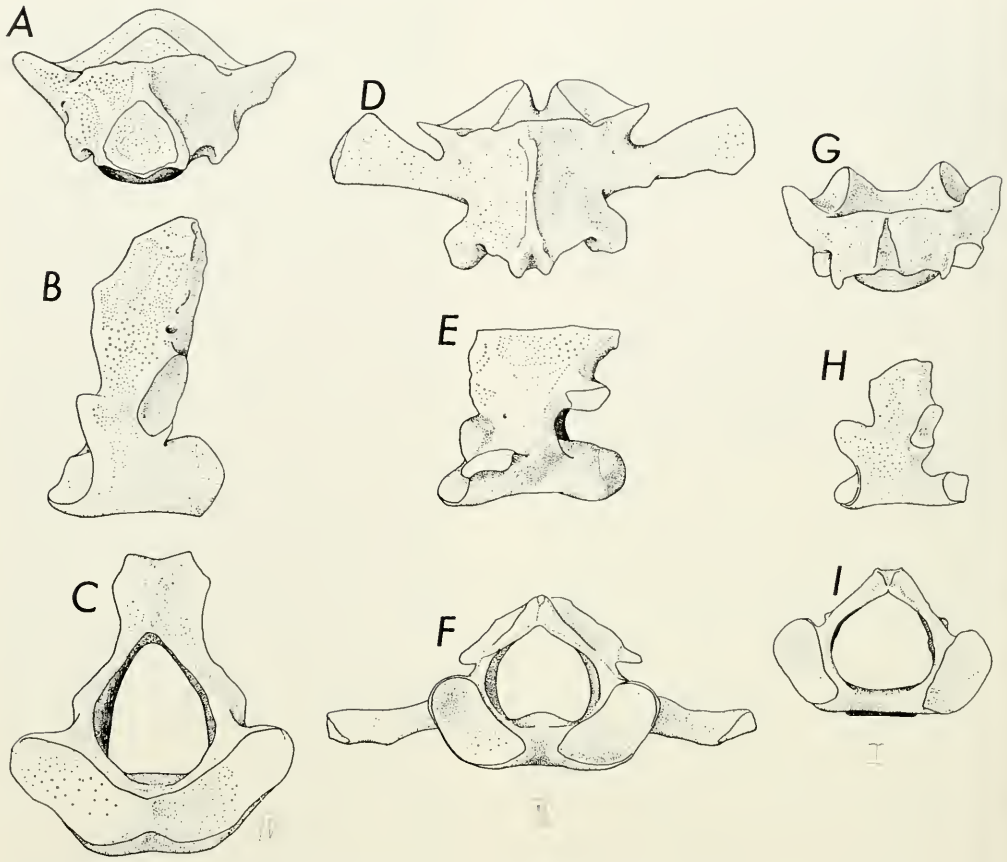

FIGURE 28. Three patterns of atlantal cotylar arrangements. (A-C) Dorsal, lateral, and anterior views of cervical vertebra of *Ceratophrys calcarata* (JDL S-237), (D-F) *Limnodynastes dorsalis* (UMMZ S-165), and (G-I) *Eleutherodactylus rugulosus* (JDL S-1238); Types III, II, and I, respectively. All $\times$ 5.

This pattern is the most widespread in leptodactylids and advanced frogs. In this class, the cotyles are sometimes stalked; when they are stalked, there is a prominent gap between the cervical vertebra and exoccipital bridge (Fig. 29).

Type II: the cervical cotyles are narrowly separated and there are two distinct articular surfaces. In many species, there is a deep notch between the cotyles (Fig. 28D). In most of the frogs with a type II cervical, the occipital condyles are clearly discrete articular surfaces.

Type III: the cervical cotyles are confluent and represent a single articular surface. The occipital condyles are confluent and the occipital-cervical articular pattern is hererocoelus. Only two leptodactylid genera *(Ceratophrys* and *Lepidobatrachus)* have a type III cervical vertebra. Consistent fusion of the cervical and second vertebrae is found in eight Australo-Papuan and African genera with type II cervicals.

Type II cervical vertebrae occur in *Adelotus, Batrachophrynus, Caudiverbera, Cyclorana, Eupsophus, Heleioporus, Heleophryne, Kyarranus, Limnodynastes, Megaelosia, Mixophyes, Neobatrachus, Notaden, Philoria, Proceratophrys, Telmatobius,* and *Telmatobufo.* The Oligocene *Neoprocoela* has a type II cervical. The occipital condyles are very large in *Limnomedusa, Odontophrynus,* and *Pleurodema;* the cervical

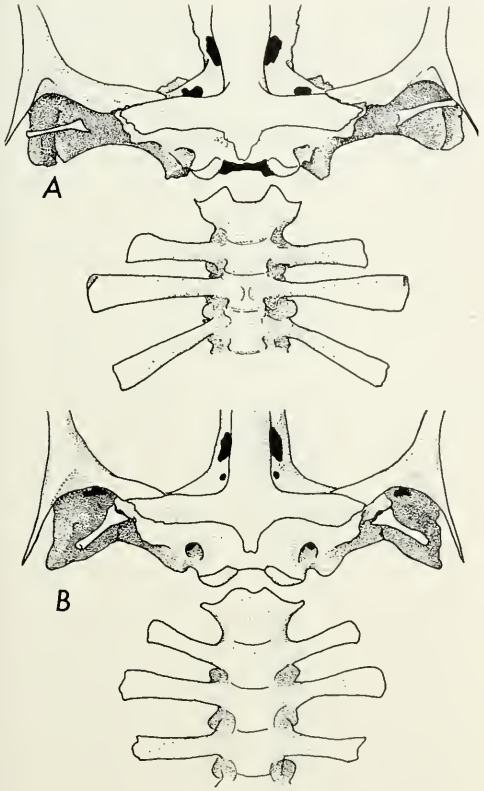

FIGURE 29. The two occipital-cervical articulation types in the Leptodactylidae. (A) *Eleutherodactylus sulcatus*, KU 100355, × 2; and (B) *Cyclorana australis*, KU 93550, × 2.

pattern is intermediate between type I and type II cervical patterns. In all other leptodactylid genera, the type I cervical is uniformly present.

The Australo-Papuan Cycloraninae all have type II cervical vertebrae, and the Myobatrachinae all have type I cervical vertebrae. One genus of the Elosiinae has a type II cervical *(Megaelosia)*, and the other two genera have type I cervical vertebrae. The Leptodactylinae have only type I cervical vertebrae, although two genera *(Limnomedusa* and *Pleurodema)* have an intermediate type cervical. In the largest leptodactylid subfamily, the Telmatobiinae, type II cervicals are found in all of the genera of the Telmatobiini, in two of the four genera of the Alsodini, and in one of the genera of the Odontophrynini. Only type I cervicals are found in the Grypiscini and Eleutherodactylini. The cervical vertebral type seems to be very useful in ascertaining the relationships of leptodactylids. The type II cervical is probably primitive, as evidenced by the uniform occurrence of this type in the archaic frog families and Pelobatidae. Type II cervical vertebrae are also characteristic of the Bufonidae and Rhinodermatidae.

Presacral vertebrae.—Hecht (1960) pointed out that the primitive frogs have very short transverse processes on the posterior presacral vertebrae, and principally for this reason he associated *Eorubeta* (Eocene) with the advanced frog families. Zweifel (1956a) demonstrated that some of the pelobatids of the subfamily Megophryinae have long transverse processes of the posterior presacral vertebrae (as long as the sacral diapophyses) and very long (here termed expanded) transverse processes of the anterior presacral vertebrae. Some Megophryinae have short posterior presacral vertebral transverse processes (*Leptobrachium*, Boulenger, 1908). As noted by Hecht (1960) the transverse processes of the posterior presacral vertebrae of most leptodactylids are as long as or only slightly shorter than the sacral diapophyses. However, in several of the more primitive leptodactylid genera, the transverse processes of the posterior presacral vertebrae are shortened to varying degrees (Fig. 30). The transverse processes of the anterior presacral vertebrae seem to vary in length independently of the variation in the length of the transverse processes of the posterior presacral vertebrae. The shortening of the transverse processes of the anterior presacral vertebrae and the concurrent lengthening of the transverse processes of the posterior presacral vertebrae represent an evolutionary trend in frogs. The transverse processes of the anterior (second, third, and fourth) presacral vertebrae are widely expanded (much wider than the width of the

sacral diapophyses) in *Ceratophrys* and *Lepidobatrachus*. The transverse processes of the anterior presacral vertebrae are slightly expanded in *Cyclorana, Odontophrynus, Proceratophrys,* and *Telmatobufo*. The transverse processes of the anterior presacral vertebrae are not wider than the width of the sacral vertebrae in all other leptodactylids and are shortened (their greatest width is less than the width of the sacral diapophyses) in *Crinia* and *Pseudophryne* (Fig. 31).

The transverse processes of the posterior presacral vertebrae are greatly shortened (knob-like) in *Neobatrachus* and *Notaden* (Fig. 30), very short (less than one-half the width of the sacral

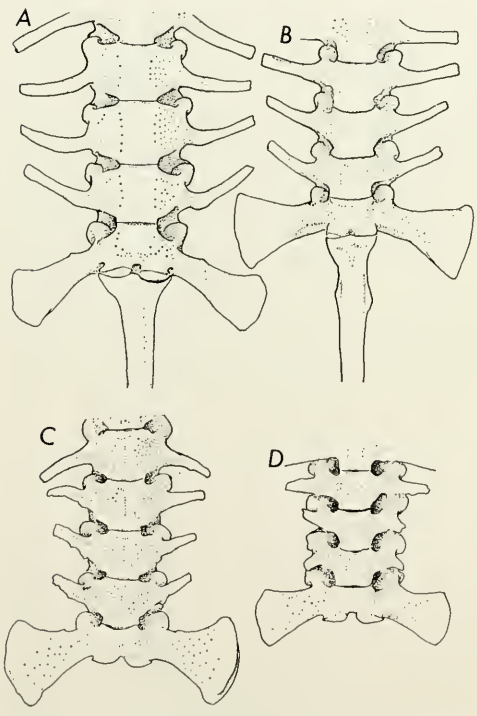

FIGURE 30. Posterior vertebral columns of four genera of cycloranine leptodactylids illustrating reduction in transverse processes in advanced Cycloranini, and presence of lateral flanges on urostyle in primitive genera of subfamily. (A) *Limnodynastes tasmaniensis*, AMNH 60589, × 5; (B) *Cyclorana australis*, KU 93550, × 2.5; (C) *Heleioporus eyeri*, UMMZ 124504, × 2.5; and (D) *Neobatrachus centralis*, KU 93578, × 2.5.

diapophyses) in *Crinia, Heleioporus, Lepidobatrachus,* and *Pseudophryne,* and moderately to slightly shortened in *Caudiverbera, Ceratophrys, Cyclorana, Cycloramphus, Eupsophus, Glauertia, Heleophryne, Myobatrachus, Odontophrynus, Proceratophrys,* and *Uperoleia*. In all the other 39 leptodactylid genera, the transverse processes of the posterior presacral vertebrae are as wide as the sacral diapophyses.

Ceratophrys and *Lepidobatrachus* have a bony shield overlaying the second, third, and fourth vertebrae (Fig. 31). In *Ceratophrys,* the shield is attached to the neural spines by ligaments. Among the species of *Ceratophrys,* there is little variation in the size and shape of the shield; some species of the genus have been reported to lack a dorsal shield, but I have not seen any adult *Ceratophrys* that lack the shield, although most juveniles of *Ceratophrys* lack a vertebral shield. In *Ceratophrys,* the shield is a loosely consolidated plate of osteoderms. Based on limited observations, the number of elements in the plate is reduced by fusion of adjacent plates with increasing age. I have not seen any specimens with only one or two elements in the shield. Dermostosis of the shield occurs in both genera. In *Lepidobatrachus laevis,* the shield is small and fused to the neural spines; the shield is larger in *L. asper* and *L. llanensis* and is connected to the vertebrae by ligaments (Reig, 1960b, Reig and Cei, 1963).

Sacral vertebrae.—The sacro-coccygeal articulation is bicondylar in all leptodactylids including the African and Australo-Papuan genera with ectochordal vertebral columns. Several authors (Noble, 1930, 1931, Schaeffer, 1949) noted the differences in the dilation of the sacral vertebral diapophyses. Schaeffer (1949) implied that all Australo-Papuan leptodactylid genera had dilated sacral diapophyses and all Neotropical genera had narrow (rounded) sacral diapophyses. Noble (1931) and Reig

(1960a) pointed out that at least some of the Neotropical genera characteristically have dilated sacral diapophyses.

The sacral diapophyses are broadly dilated in all pelobatids, bufonids, and most hylids. The fossil Oligocene leptodactylid, *Neoprocoela*, has broadly dilated sacral diapophyses, as does the enigmatic Chilean *Rhinoderma*. No extant leptodactylid genus has broadly dilated sacral diapophyses, although it is impossible to place lower limits on

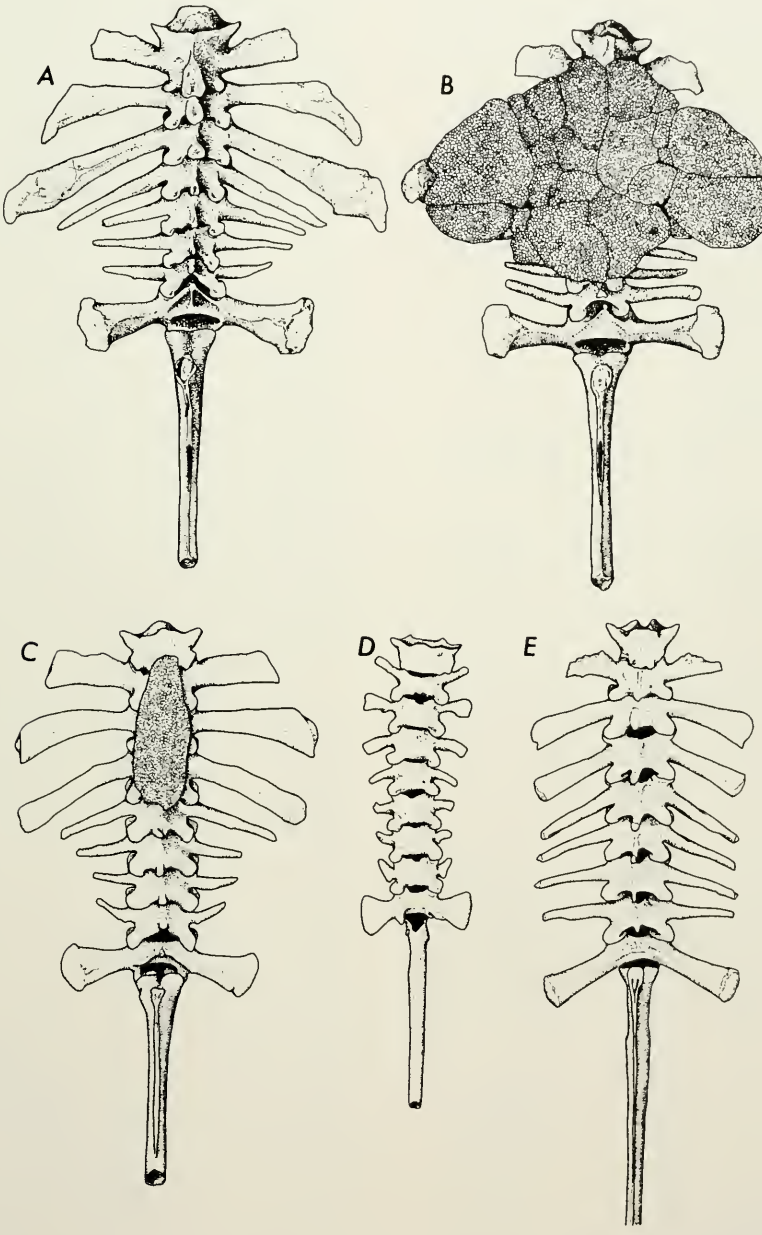

FIGURE 31. Vertebral columns of (A-B) *Ceratophrys aurita*, A has the bony shield removed (KU 98129, × 0.9; FMNH 51704, × .9), (C) *Lepidobatrachus asper* (KU 80783, × 2.2), (D) *Crinia signifera* (KU 56243, × 6.4) and (E) *Leptodactylus pentadactylus* (KU 68159, × 0.9).

the character of "dilated sacral diapophyses." The sacral diapophyses are moderately dilated in all of the Australo-Papuan genera and in eight Neotropical genera *(Batrachyla, Caudiverbera, Crossodactylodes, Edalorhina, Eupsophus, Odontophrynus, Physalaemus,* and *Pleurodema).* Any distinction between the degree of dilation exhibited by some of the above-mentioned genera and such leptodactylids as *Ceratophrys* and *Paratelmatobius* is a very fine one and probably is not defensible. The majority of the African and Neotropical leptodactylid genera have rounded, undilated sacral diapophyses which are either perpendicular to the sagittal plane or slanted posteriorly (Fig. 32).

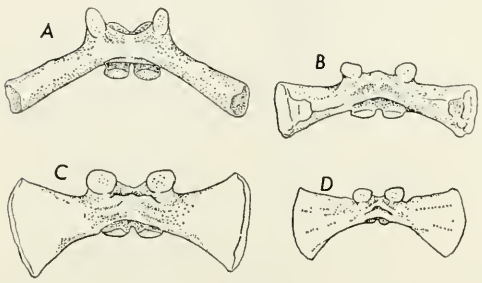

FIGURE 32. Sacral vertebrae of leptodactylids and a bufonid illustrating the degree of expansion of the sacral diapophyses. (A) *Eleutherodactylus rugulosus* (JDL S-1238, × 4), (B) *Odontophrynus cultripes* (KU 92975, × 2.5), (C) *Cyclorana dahli* (UMMZ 65250, × 3), and (D) *Bufo marmoreus* (KU 84894, × 2).

Coccyx.—I have not observed zygapophyseal processes on the anterior portion of the coccyx of any leptodactylid, although S. B. McDowell (in litt.) has observed prezygapophyseal processes on the coccyx of *Metacrinia.* The coccyx is short and stocky in several genera; nerve foramina are evident on the anterolateral surface of the coccyx in several leptodactylids. Neither of these characters shows a clear trend but appears sporadically among the species I have examined. *Batrachophrynus* has large transverse processes at the anterior end of the coccyx (Fig. 79).

In the Elosiinae, the neural arches are distinctly non-imbricate and poorly ossified. The roof of the neural canal of the coccyx is likewise poorly ossified.

Pectoral Girdle

The primary basis for the divisions of the advanced frogs by Cope and Boulenger was the variation in the architecture of the pectoral girdle. The two divisions, the Arcifera and Firmisterna, differ in the overlapping epicoracoidal cartilages in the former and the median fusion of the epicoracoidal cartilages in the latter. Noble (1921, 1922, 1931) severely criticized the Cope-Boulenger system after he found several South American frogs with intermediate types of pectoral girdles. Griffiths (1959, 1963) redefined the terms arciferal and firmisternal on the basis of the presence (arciferal) or absence (firmisternal) of free epicoracoidal horns. Griffiths also pointed out that the two types of pectoral girdles have different developmental patterns.

When the primary basis of frog classification changed from the pectoral girdle to the vertebral column and thigh musculature, relatively few groups shifted between the Arcifera (=Procoela and Bufonoidea) and the Firmisterna (=Diplasiocoela and Ranoidea). The Dendrobatidae, *Geobatrachus, Rhinoderma,* and *Sminthillus (Euparkerella, Noblella,* and *Sminthillus)* were alternately associated with the Bufonoidea and the Ranoidea. Noble (1926b and 1931) considered all of these genera to be bufonid derivatives, whereas Griffiths (1959) considered the dendrobatids to be a Neotropical subfamily of the Ranidae, *Geobatrachus* and *Rhinoderma* to be the only members of a Neotropical leptodactylid subfamily, and *Sminthillus* to be a polyphyletic assemblage of *Eleutherodactylus* derivatives.

Most leptodactylid frogs are clearly arciferal (in either Cope's sense or Griffiths' sense). Prior to the refinement of the distinction between arcifery and firmisterny, the leptodactylid frogs of the genera *Sminthillus* and *Noblella* were

characterized by their arcifero-firmisternal pectoral girdles. Noble (1921, 1922, 1926b, 1931) considered the epicoracoidal cartilages of *Sminthillus* to be fused from a point at the base of the omosternum to the anterior edge of the coracoid, whereas Griffiths (1959) found that the epicoracoidal bridge was restricted to the anterior-most portion of the cartilages and always restricted to a narrow zone anterior to or between clavicles. I have found epicoracoidal bridges in both small and large species, but the fusion is most often found in the smaller specimens, because one tends to be less meticulous in the dissection of larger specimens. All leptodactylids have discrete epicoracoidal horns which are usually partially concealed by the sternum. Hoffman (1930) reported *Heleophryne* to pass from arcifery in juveniles and subadults to firmisterny in adults. Poynton (1964) pointed out that *Heleophryne* is always arciferal and that Hoffman's "old adult *Heleophryne*" was a specimen of a ranid (either *Hylambates* or *Leptopelis*). All other leptodactylid genera are, and have always been, regarded as arciferal in the sense of Cope and Boulenger.[4]

The relative bulk of the clavicle and coracoid, the presence of an omosternum, and the presence of an osseous sternal (post-zonal) element are variable characters in the pectoral girdles of leptodactylid frogs. Piatt (1934) distinguished three types of omosterna and three types of sterna in 35 species of leptodactylids *(Eleutherodactylus, Leptodactylus,* and *Lithodytes)* based on the character states uniformly cartilaginous, partly calcified, and containing an osseous element. I am unwilling to place much taxonomic weight on small variations in the size of the omosternum and sternum, or on the distinction between uniformly cartilaginous and partly calcified. Calcification of the sternum occurs in large females of several species in which the sternum of the smaller male is uniformly cartilaginous. The larger specimens of a given species are more likely to have some calcification of the sternal plate than are the smaller specimens of the species. In several leptodactylid genera, the differences in the average adult size of the various species of that genus are reflected in the presence and absence of calcification of the sternum and often of the omosternum and epicoracoidal cartilages. Although fully cognizant of the limitations of both, I consider the following characters to be useful in distinguishing the genera of leptodactylids: 1) presence of a cartilaginous or calcified sternal plate *versus* the presence of a discrete osseous sternal element (usually a style) and 2) presence of an omosternum.

The sternum in most leptodactylids is a cartilaginous plate (Fig. 33); in the Neotropical Leptodactylinae *(Barycholos, Edalorhina, Hydrolaetare, Leptodactylus, Limnomedusa, Lithodytes, Paratelmatobius, Physalaemus, Pleurodema,* and *Pseudopaludicola)* the sternum contains an osseous (or calcified) style or an osseous plate *(Paratelmatobius). Lithodytes* also has an osseous style in the omosternum; the omosternum is cartilaginous in all of the other genera.

Parker (1940) reported that the omosternum was reduced in size or absent in all Australo-Papuan leptodactylids. In the Australo-Papuan genera *Adelotus, Cyclorana, Lechriodus, Limnodynastes,* and *Mixophyes,* the omosternum is large to moderately large (Fig. 33). The omo-

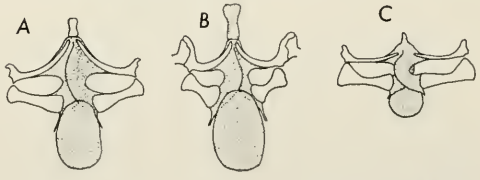

FIGURE 33. Pectoral girdles of (A) *Heleophryne natalensis* (KU 105925, × 1.5), (B) *Limnodynastes peronii* (KU 93562, × 1.2), and (C) *Crinia signifera* (KU 56317, × 4).

[4] Barrio (1970) named a new Chilean genus *(Insuetophrynus)* with a pseudofirmisternal pectoral girdle similar to that seen in some *Atelopus,* but having a well-developed prezonal element.

sternum is absent in *Myobatrachus* and reduced in size in the other Australo-Papuan genera of the Myobatrachinae and the cycloranine genera *Heleioporus, Kyarranus, Neobatrachus, Notaden,* and *Philoria.* The omosternum in *Crinia* is usually elongate and not separable from the anterior extent of the epicoracoidal cartilages (Fig. 33). The omosternum is present in all other leptodactylids that I have examined except *Lepidobatrachus, Odontophrynus, Proceratophrys,* and *Eleutherodactylus ruthae,* although the omosternum is small in several species of the West Indian *Eleutherodactylus.* The omosternum is unusually large—often larger than the sternum—

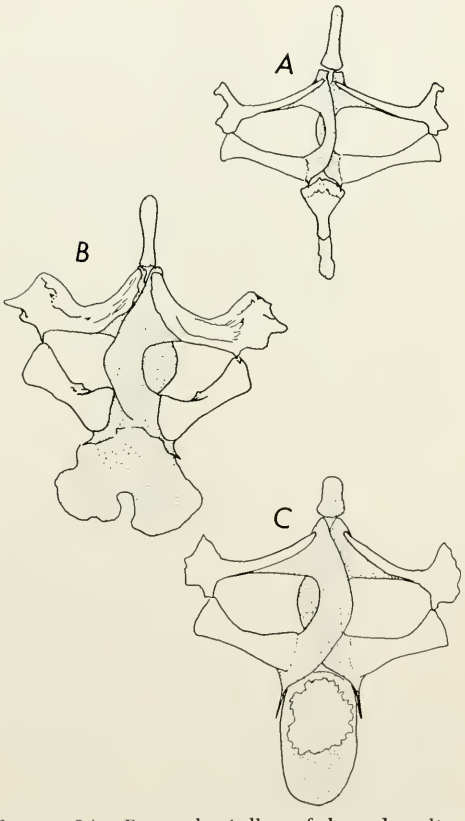

FIGURE 34. Pectoral girdles of leptodactyline leptodactylid (A) *Pseudopaludicola ameghini* (KU 93050, × 5.5) and two telmatobiines (B) *Telmatobius hautholi* (KU 72879, × 2) and (C) *Eleutherodactylus bogotensis* (KU 110409, × 4).

in a few Neotropical leptodactylids *(Ceratophrys* and *Telmatobufo).*

The clavicles are large and strongly arched in the Neotropical genera *Caudiverbera, Telmatobius,* and *Telmatobufo,* and are very slender and fragile in many of the smaller species of leptodactylids (Fig. 34). In most species of the family, the clavicles are neither massive nor fragile. The clavicles are relatively straight in most Neotropical leptodactylids (except the Ceratophryinae and Telmatobiini) and many Cycloraninae. In most myobatrachines the clavicles are slender and strongly arched (Fig. 33) but in *Myobatrachus* the clavicles are massive and only slightly arched.

The following generalizations concerning the architecture of the leptodactylid pectoral girdle are suggested: 1) arcifery is the primitive character state —pseudofirmisterny is derived and of little taxonomic significance; 2) an osseous element in either the pre-zonal or post-zonal element is secondary to uniformly cartilaginous elements; calcification of the sternal plate is a labile feature; and 3) primitively, the omosternum is large—reduction in size or loss of the omosternum is derived.

The osseous post-zonal elements of leptodactylines are primitively broad and become more style-like in the advanced genera (Fig. 35). Posterior bifurcation of the style is derived.

Pelvic Girdle

The pectoral girdle has long been recognized as an important complex for systematic studies of anurans whereas few authors sought to find characters in the simpler pelvic girdle, which is more closely associated with the primary adaptive shift of frogs—jumping. The anuran pelvis is composed of three elements (ilium, ischium, and pubis) of which only the ilium exhibits familial or consistent generic variation. Some paleontologists (e.g., Auffenberg, Chantell, Estes, Holman, and Tihen) considered the ilium of paramount importance in

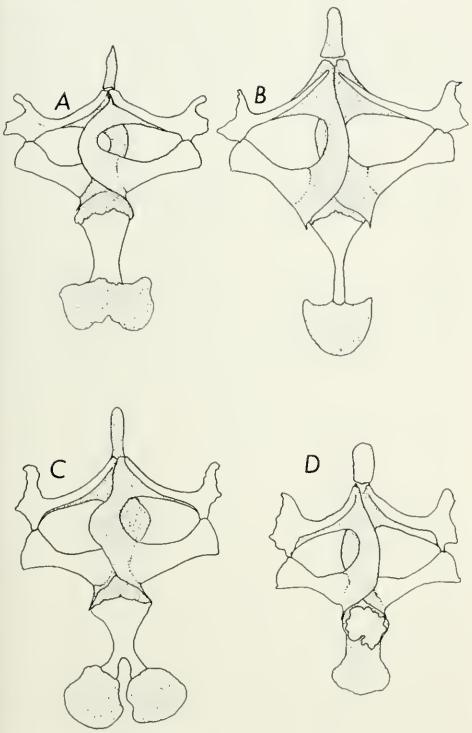

FIGURE 35. Pectoral girdles of four leptodactyline leptodactylids. (A) *Physalaemus pustulosus* (KU 68272, × 5.5), (B) *Leptodactylus melanonotus* (KU 68276, × 3), (C) *Physalaemus signiferus* (KU 93033, × 5.5), and (D) *Paratelmatobius lutzi* (KU 107089, × 5.5).

the identification of disarticulated frog fossils at the familial, generic, and, in some cases, specific level. Brief references were made by some of these authors to the range of variation exhibited by the leptodactylid genera.

Holman (1965) noted the variation in development of the ilial crest and in the size and shape of the ilial prominence (termed by him, vastus prominence). The nomenclature for the ilial morphology adopted here follows that of Chantell (1964) and is illustrated for leptodactylid frogs in Figure 36. The only additional term employed here is the "preacetabular zone"—that area of the ventral acetabular expansion lying anterior to the lip of the acetabulum and dorsad to the ventral lip of the acetabulum.

Owing to the diverse forms of the ilium in leptodactylids, no familial diagnosis can be made at this time. The relatively few genera available support this conclusion. Skeletons of the following genera were available: *Adelotus, Barycholos, Batrachophrynus, Caudiverbera, Ceratophrys, Crossodactylus, Cycloramphus, Cyclorana, Edalorhina, Eleutherodactylus, Eupsophus, Heleioporus, Hylactophryne, Hylodes, Ischnocnema, Kyarranus, Lechroidus, Lepidobatrachus, Leptodactylus, Limnodynastes, Limnomedusa, Megaelosia, Neobatrachus, Notaden, Odontophrynus, Physalaemus, Pleurodema, Proceratophrys, Pseudophryne, Syrrhophus, Telmatobius, Thoropa, Tomodactylus,* and *Zachaenus.*

The two ilial types are briefly described below.

Ceratophryine type: ilial shaft relatively short; dorsal crest not developed, if present, in form of ilial shaft ridge; dorsal protuberance not, or but slightly, differentiated from spike-like dorsal prominence; dorsal acetabular expansion well developed, distinct dorsal vector; preacetabular zone present, broad; ventral acetabular expansion relatively

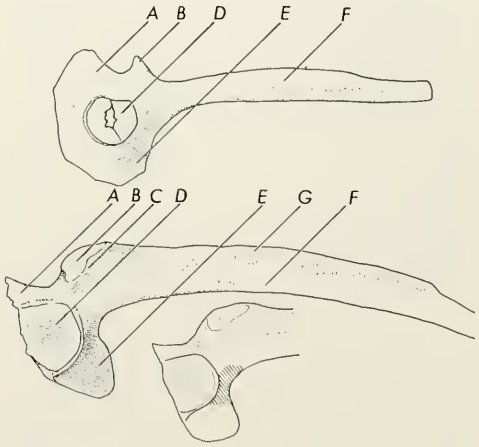

FIGURE 36. Nomenclature of the leptodactylid ilium. Top is ilium of *Ceratophrys ornata* (genus lacking dorsal crest); middle is that of *Leptodactylus pentadactylus* (genus with dorsal crest). (A) dorsal acetabular expansion; (B) dorsal protuberance (vastus prominence of Holman); (C) dorsal prominence; (D) acetabular fossa; (E) ventral acetabular expansion; (F) shaft; (G) dorsal crest. The preacetabular zone is hatched in the lower figure.

small; angle of ventral acetabular expansion greater than 90°; acetabular fossa relatively small (Fig. 37).

Leptodactyline type: ilial shaft relatively long; dorsal crest well developed, usually higher anteriorly and in the region of dorsal protuberance; dorsal protuberance relatively large [vastus prominence of Holman (1965)], ovoid, or tear-drop-shaped, situated on a large dorsal prominence which is confluent with dorsal crest; posterior border of dorsal prominence gently sloping; dorsal acetabular expansion not well developed, little or no dorsal vector; preacetabular zone present, broad; ventral acetabular expansion relatively large; angle of ventral acetabular expansion much less than 90°; acetabular fossa relatively large (Fig. 37).

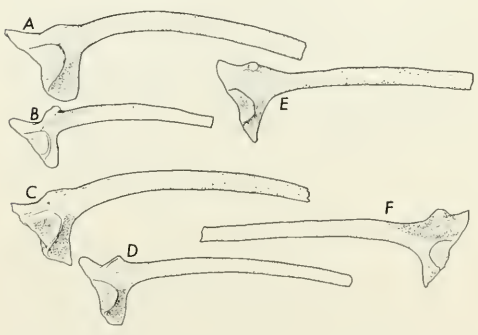

Figure 37. Right ilia of (A) *Pseudophryne bibroni*, AMNH 64511, × 5.4; (B) *Adelotus brevis*, AMNH 59489, ×1.6; (C) *Cyclorana australis*, AMNH 62228, × 1.2; (D) *Limnodynastes dorsalis*, KU 93553, × 1.6; (E) left ilium of *Neobatrachus centralis*, KU 93578, × 1.6; and (F) right ilium of *Notaden bennetti*, FMNH 97858, × 1.2.

The ilia of the two genera of the Ceratophryinae are nearly impossible to separate. *Lepidobatrachus* has a more distinct ilial shaft ridge than does *Ceratophrys* and a slightly less pronounced dorsal prominence (spike); too few specimens are available to make a generalization. *Odontophrynus* and *Proceratophrys* (Telmatobiinae, Odontophrynini) are the only other Neotropical genera examined which have the ceratophryine pattern. Both genera differ from the Ceratophryinae in having a more distinct dorsal protuberance, larger ventral acetabular expansion, and less obtuse angle of ventral acetabular expansion (Fig. 38).

Several cycloranine genera have ilia which differ only slightly from the ceratophryine pattern. All Australo-Papuan genera examined have a relatively large angle of ventral acetabular expansion (90-110°) and relatively small acetabular fossa. The dorsal prominence is never spike-like and most genera have a distinguishable dorsal protuberance (e.g., *Adelotus, Heleioporus, Lechriodus,* and *Neobatrachus*). The dorsal protuberances of *Kyarranus* and *Limnodynastes* are only slightly less differentiated, but those of *Cyclorana, Notaden* and the myobatrachines are not distinguishable from the dorsal prominence. Dorsal crests are lacking in the myobatrachines, and all cycloranines examined except *Adelotus, Kyarranus,* and *Lechriodus* (Fig. 38).

The angle of ventral acetabular expansion is slightly greater than 90° in *Caudiverbera, Edalorhina, Eleutherodactylus, Engystomops, Eupsophus, Hylactophryne, Limnomedusa, Pleurodema, Syrrhophus, Tomodactylus,* and *Zachaenus*, whereas it is markedly acute in *Crossodactylus, Cycloramphus, Hylodes, Leptodactylus, Megaelosia,* and *Thoropa*. In *Batrachophrynus, Ischnocnema,* and *Telmatobius* it is about 90°.

The dorsal crest is absent in *Edalorhina, Eupsophus, Physalaemus,* and *Pleurodema*. In some *Eleutherodactylus* and the Mexican *Syrrhophus* and *Tomodactylus,* the dorsal crest is reduced to a small area immediately anterior to the dorsal prominence. This latter condition is also seen in *Limnomedusa*. The dorsal crest is well developed in *Caudiverbera, Crossodactylus, Cycloramphus,* most *Eleutherodactylus, Hylactophryne, Hylodes, Ischnocnema, Leptodactylus, Megaelosia,* and *Zachaenus*; in *Batrachophrynus, Telmatobius,* and *Thoropa*

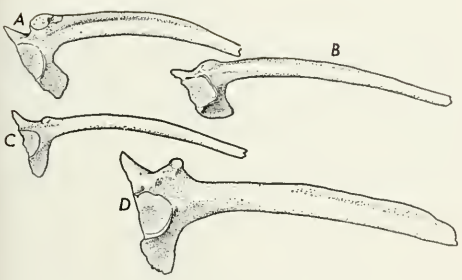

FIGURE 38. Right ilia of (A) *Hylodes nasus*, KU 92894, × 2.1; (B) *Thoropa miliaris*, KU 92856, × 1.6; (C) *Eupsophus roseus*, AMNH 22104, × 1.6; and (D) *Odontophrynus cultripes*, KU 92975, × 1.6.

it is low and almost ridge-like (Figs. 37-40).

The dorsal protuberance is well developed in all elosiine, leptodactyline, and telmatobiine frogs examined except *Megaelosia* and *Pleurodema*. In these latter two genera, the muscle scar for the *vastus externus* head of the *m. triceps femoris* is broad and covers the whole of the dorsal prominence. The protuberance is ovoid, round, or elongate, and no characterization of genera can be made owing to the variability of the protuberance in *Eleutherodactylus*.

The degree of dorsal vector in the dorsal acetabular expansion shows some variation in the Neotropical leptodactylids. Almost no dorsal vector is seen in *Batrachophrynus, Edalorhina, Leptodactylus, Pleurodema, Telmatobius*, and *Thoropa*, whereas the other genera exhibit a considerable dorsal vector. *Eleutherodactylus palmeri* (Fig. 39), in contrast to the other species of the genus examined, has no dorsal vector and the dorsal crest appears to be lacking but is present and curved over the body of the ilial shaft.

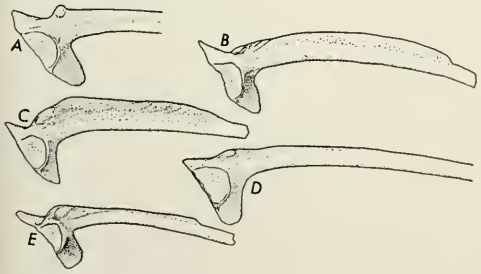

FIGURE 39. Right ilia of (A) *Eleutherodactylus diastema*, JDL S-244, × 6.6; (B) *E. inoptatus*, AS X2356, × 1.2; (C) *E. rugulosus fleischmanni*, KU 68157, × 1.2; (D) *E. palmeri*, JDL S-242, × 3.3; and (E) *Cycloramphus fulginosus*, KU 92790, × 1.2.

The ilium seems to have some merit in suggesting relationships among the leptodactylid genera, but at this time inadequate data are available in order to incorporate the variation of the ilium into my generic classification. In some cases (Ceratophryinae and Elosiinae), the ilial variation is consistent with the variations of other character complexes, but in other cases (Leptodactylinae),

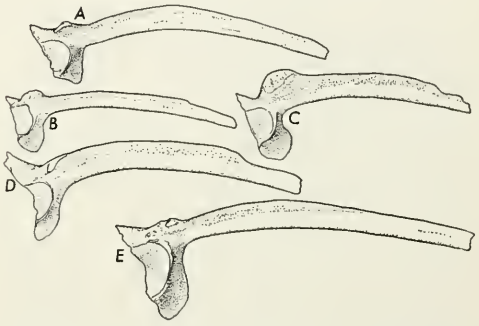

FIGURE 40. Right ilia of (A) *Physalaemus pustulosus*, KU 41031, × 5.4; (B) *Pleurodema cinerea*, KU 80836, × 1.6; (C) *Leptodactylus wagneri*, KU 104390, × 1.2; (D) *Caudiverbera caudiverbera*, A.M.N.H. No. 51510, × 0.6; and (E) *Batrachophrynus macrostomus*, KU 98127, × 0.6.

the variation is not consistent with my other data. Owing to these discordancies, use of the ilium in a leptodactylid classification is deferred pending a broader survey of the variation in the ilia of other leptodactylid frogs.

The data now available are adequate to permit a reassessment of the status of a Lower Miocene *Leptodactylus* recently described from Florida. Holman (1965) named *L. abavus* based on five ilia from the Arikareean horizon of Thomas Farm, Gilchrist County, Florida. The frog he described and figured has almost no preacetabular zone, a moderately large angle of ventral acetabular expansion, and a small ventral acetabular expan-

sion. These characteristics are not typical of *Leptodactylus* but are typical of *Rana*—especially the species of the *R. pipiens* group. There is a marked similarity between his figures of the ilia of *Leptodactylus abavus, Rana miocenica,* and *Rana* cf. *R. pipiens. Leptodactylus abavus* Holman, 1965, is accordingly here removed from the family Leptodactylidae and placed in the Ranidae. The specific status of *Rana abavus* (Holman), new combination, is beyond the scope of this paper, but at present, there are no apparent differences between it and *Rana miocenica,* a sympatrant.

Limb Elements

To a certain extent, the mode of life of a frog is reflected in the proportions of the long bones (humerus, radioulna, femur, tibiofibula, and astragulus and calcaneum). Species living in páramos and those with burrowing habits tend to have heavier, stockier long bones than do the arboreal or active terrestrial frogs, in which the limb bones are relatively slender. Those differences that do exist are subtle and offer little in the way of taxonomic utility. Because the characters seem more reasonably associated with ecological adaptation, they are not regarded as useful in a phylogenetic classification. The intrageneric variation in *Eleutherodactylus* precludes the use of relative proportions of the limb elements for generic or suprageneric classifications.

The greatly enlarged arms of males of some species of *Leptodactylus* have been noted by several authors. The skeletal base for the sexual dimorphism is considerably more striking. Large flanges are present on the humeri of the male, whereas the female has humeri more typical of frogs (Fig. 41). Development of humeral flanges is uncommon in the Leptodactylidae, and is most pronounced in the genus *Leptodactylus.* The development of humeral flanges in *Leptodactylus* appears to be species-group variable and therefore may prove useful in subgeneric classifications. Moderate flanges are seen in the *Eupsophus nodosus* group, again restricted to the male (Grandison, 1961), in *Crossodactylodes, Paratelmatobius,* some *Physalaemus,* and *Telmatobius* (Fig. 41).

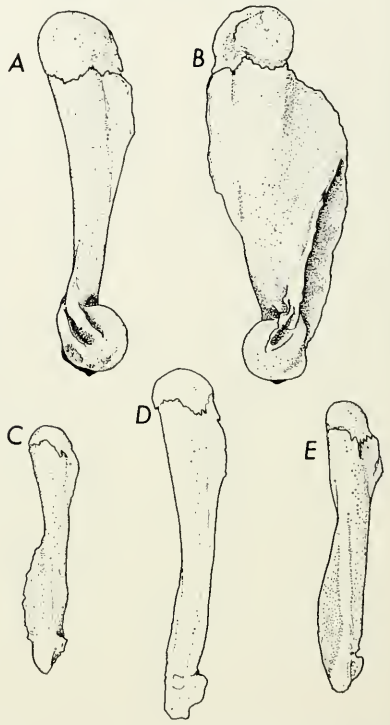

FIGURE 41. Humeri of (A) female *Leptodactylus pentadactylus* (lateral view of right humerus, KU 68159, × 0.8) and (B) male *L. pentadactylus* (lateral view of left humerus, KU 84981, × 0.8); medial views of left humeri of male (C) *Physalaemus signiferus* (KU 93033, × 4.8), (D) *P. cuvieri* (KU 92999, × 4.8), and (E) *Paratelmatobius lutzi* (KU 107089, × 4.8).

Phalangeal formulae.—The primitive phalangeal formulae of the Leptodactylidae are 2-2-3-3 for the hand and 2-2-3-4-3 for the foot. Phalangeal reduction is often regarded as a character *sui generis* in amphibian classifications, because it is a relatively uncommon phenomenon. The only variations on the above formulae in the Leptodactylidae are seen in *Euparkerella* which has a 2-2-3-2 formula for the hands and a normal foot formula (Figs. 42-43) and in *Limnodynastes peronii* which has a 1-2-3-3 hand for-

mula (all other *Limnodynastes* have a 2-2-3-3). Parker (1940) and Moore (1961) briefly mentioned that the digits were reduced in some of the myobatrachine leptodactylids (*Crinia* and *Pseudophryne*). In external appearance, the digits are short and stubby, but the phalangeal formulae are typical for bufonoid frogs (2-2-3-3, 2-2-3-4-3).

Terminal Phalanges.—The nature of the terminal phalanges has been one of the major character complexes in leptodactylid classification. Generic diagnoses invariably contain reference to "simple, pointed, knobbed or T-shaped" terminal phalanges.

Based on a literature study, there seems to be a wide range of terminal phalangeal types within the Leptodactylidae. The phalangeal types are termed pointed, simple, knobbed, bifurcate, Y-shaped, and T-shaped. In the past, the technique for observing the terminal phalanges was to dissect the digital tip and observe the shape of the bone. Since the terminal phalanges are often very small and delicate, dissection tends to break any lateral expansions. Observations of the bones with the naked eye often fails to discern small lateral processes. In my opinion, the only technique acceptable for the observation of the terminal phalanges is examination of macerated or cleared and stained specimens. My studies, presented below, are based almost exclusively on examination of cleared and stained material.

No leptodactylid normally has pointed terminal phalanges. The most simple phalanges are very slightly knobbed (e.g., *Limnodynastes* and the *Pseudopaludicola falcipes* complex). A graded series can be demonstrated ranging from *P. falcipes* to some of the arboreal *Eleutherodactylus* with widely expanded, delicate, T-shaped terminal phalanges (Figs. 42-44).

The following genera exhibit definite T-shaped terminal phalanges in all species: *Batrachyla, Crossodactylodes* (see Fig. 44, Y-shaped), *Crossodactylus, Helleophryne, Hylodes, Lithodytes, Megaelosia, Sminthillus, Syrrhophus, Taudactylus, Thoropa,* and *Tomodactylus.* Modified T-shaped terminal phalanges are seen in *Euparkerella* (Figs. 42-43). *Barycholos* and the *Leptodactylus marmoratus* group have terminal phalanges with moderately long lateral processes. In the genus *Eleutherodactylus* there is a continuum of variation in the terminal phalanges from those of *E. binotatus* and *E. nigrovittatus* (knob-like) to that exemplified by *E. brevicrus* (broadly T-shaped). The phalangeal type of all other leptodactylids, except the *Pseudopaludicola falcipes* group and *Limnodynastes* (Fig. 45), is included in the bottom of the *Eleutherodactylus* series [for example, *Holoaden, Leptodactylus* (except *marmoratus* group), *Niceforonia,*

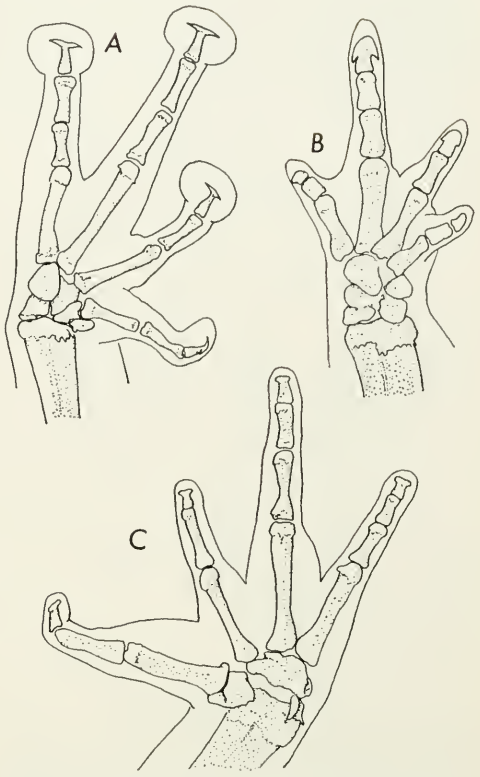

FIGURE 42. Palmer views of the skeletons of the hands of (A) *Eleutherodactylus brevicrus,* KU 108982, × 10.5; (B) *Euparkerella brasiliensis,* KU 93192, × 21); and (C) *Eleutherodactylus binotatus,* KU 92813, × 7.

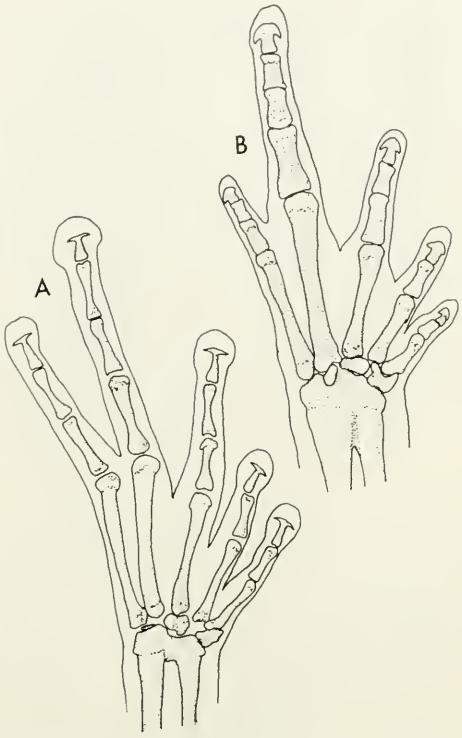

FIGURE 43. Plantar views of skeletons of feet of (A) *Eleutherodactylus bogotensis*, KU 110409, × 7; and (B) *Euparkerella brasiliensis*, KU 93192, × 21.

Paratelmatobius, Pseudophryne, Telmatobius, and *Zachaenus* (Fig. 44)].

Use of the nature of the terminal phalanges is not invalidated by the above data. Even when the lateral processes of the terminal phalanges are reduced (as in *E. binotatus* and *E. nigrovittatus*), the eleutherodactyline digital groove is evident externally. The lateral expansions of the terminal phalanges of the hands in *E. nigrovittatus, Holoaden bradei,* and *Niceforonia festae* are comparable, but there are true T-shaped terminal phalanges in *Eleutherodactylus nigrovittatus* but merely the lateral expansion of knobbed terminal phalanges in *Holoaden* and *Niceforonia* (Fig. 45). Furthermore, in *Eleutherodactylus nigrovittatus,* at the tip of each digit (except the thumb and inner toe) there is a transverse terminal groove. The degree of development of lateral expansions varies on the different digits of the hand and foot as well as between the hand and foot. When reduction of lateral expansions occurs, it is most readily observed on the hand; the toes retain relatively well developed lateral expansions. The lateral expansions of the inner digits show greater reduction than do those of the outer digits.

Prepollex and inner metacarpal.—The presence of nuptial excrescences, asperities, or spines serves as an external indicator of some modification of the first metacarpal and/or expansion or modification of the prepollex. These changes

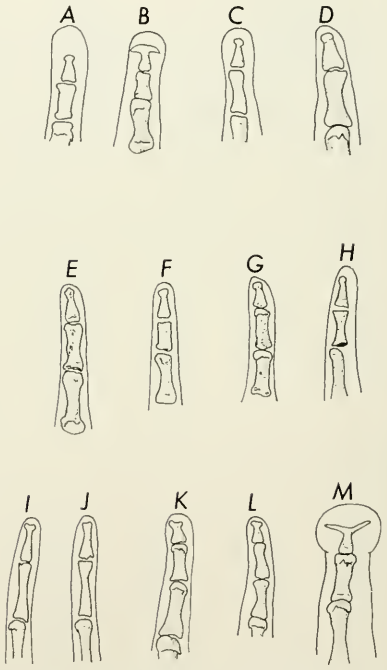

FIGURE 44. Third fingers of representative leptodactylids (A) *Eleutherodactylus nigrovittatus* (USNM GOV 8108, × 17), (B) *E. parvus* (KU 92834, × 17), (C) *Holoaden bradei* (KU 107088, × 8.5), (D) *Niceforonia festae* (KU 118137, × 17), (E) *Telmatobius hautholi* (KU 72879, × 4.2), (F) *Leptodactylus melanonotus* (KU 68275, × 5.6), (G) *Pseudophryne bibroni* (KU 93588, × 8.5), (H) *Limnodynastes peronii* (KU 93566, × 8.5), (I) *Pseudopaludicola pusilla* (UMMZ 54589, × 17), (J) *P. ameghini* (KU 93050, × 17), (K) *Zachaenus parvulus* (KU 107090, × 8.5), (L) *Paratelmatobius lutzi* (KU 107089, × 8.5), and (M) *Crossodactylodes pintoi* (USNM 102611, × 17).

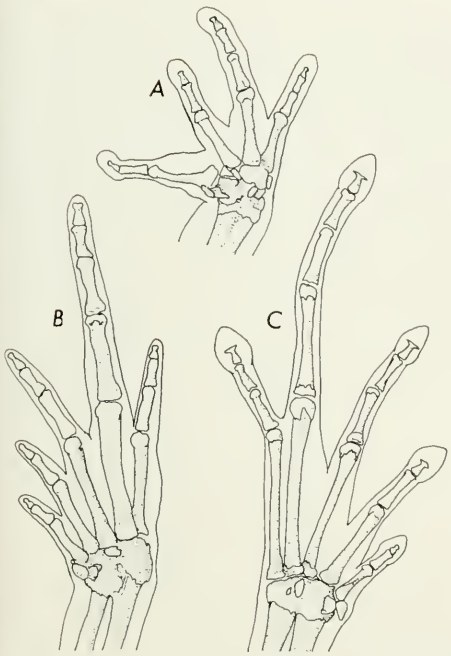

FIGURE 45. Skeletons of hand of (A) *Eleutherodactylus nigrovittatus* (USNM GOV 8108) and feet of (B) *Niceforonia festae* (KU 118137) and (C) *Eleutherodactylus nigrovittatus* (USNM GOV 8108). All × 10.5.

are not manifest in the female and while perhaps of some phylogenetic importance are not employed here. Prepollices are absent or greatly reduced in size in those genera and species which lack nuptial asperities or swelling of the thumb. In some genera (e.g., *Telmatobius*), the prepollex is greatly enlarged (Fig. 46), whereas in others with similar nuptial excrescences (e.g., *Physalaemus*), the inner metacarpal is modified for support. In those genera with large, isolated nuptial spines (e.g., *Heleioporus* and *Leptodactylus*), the inner spine is prepollical and the outer metacarpal (Fig. 46).

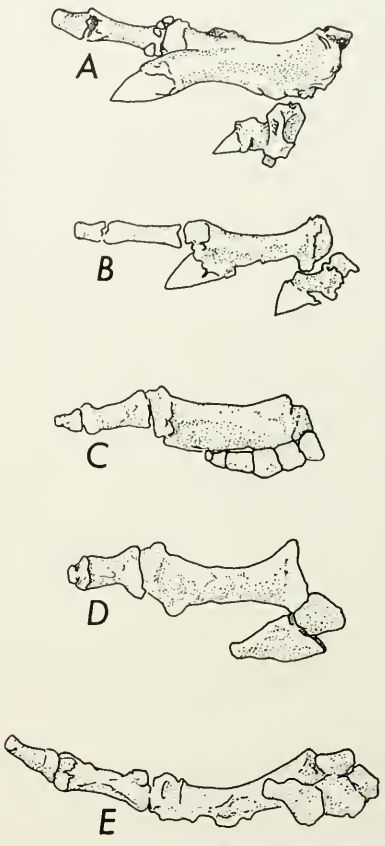

FIGURE 46. Skeletons of first finger (thumb) and prepollices of male leptodactylids. (A) *Leptodactylus pentadactylus* (KU 84981, × 1.2), (B) *L. melanonotus* (KU 68275, × 4.8), (C) *Telmatobius hautholi* (KU 72879, × 3.6), (D) *Paratelmatobius lutzi* (KU 107089, × 15), and (E) *Physalaemus signiferus* (KU 93033, × 7).

SYSTEMATIC ACCOUNTS

In the following accounts those characters which are only diagnostic at the subfamily level are listed in the subfamily accounts but not in the generic accounts. I consider it desirable to use the same sequence of character statements in all of the generic accounts, and have numbered all character or character complexes consecutively throughout the following accounts. In some cases, where the state of a character is not known for a genus, the number is retained in the diagnosis, but no statement follows it. The following characters and character complexes were used to diagnose the subfamilies, tribes, and genera recognized herein: 1) sternum cartilaginous, or bearing an osseous plate or style; 2) a dermostosed vertebral shield is present or absent; 3) the transverse processes of

the anterior presacral vertebrae are expanded or not; 4) the arrangement of the cervical cotyles; 5) cervical and second vertebrae free or fused; 6) cranial bones involved in dermostosis or not; 7) omosternum present or absent, large or small; 8) degree of dilation of sacral diapophyses; 9) maxillary arch toothed or not, teeth pointed or blunt, pedicellate or not; 10) direction of and width at the base of the alary processes of the premaxillae; 11) shape of the palatal shelf of the premaxilla; 12) size of facial lobe of maxilla; 13) shape of the palatal shelf of the maxilla, development of pterygoid process of maxilla; 14) maxillary arch complete or not, if not, quadratojugal present or absent; 15) size of nasals and degree of median contact between nasals; 16) contact of nasals and maxillae, nasals and pterygoids; 17) contact of nasals and frontoparietals; 18) frontoparietal fontanelle—present or absent; 19) ornamentation of frontoparietals; 20) fusion of frontoparietal and proötic; 21) temporal arcade present or not; if present, temporal fenestra present or not and temporal notch present or not; 22) development of epiotic eminences; 23) shape of cristae paroticae; 24) size of zygomatic ramus of squamosal; 25) size of otic ramus of squamosal, development of otic plate; 26) size of squamosal-maxillary angle; 27) columella present or absent; 28) prevomers toothed or not, in median contact or not, and position of dentigerous processes relative to choanae; 29) median and lateral extent of palatines, development of odontoids; 30) sphenethmoid divided or entire, shape and extent anteriorly; 31) shape of anterior ramus of parasphenoid, keeled medially or not; 32) degree of overlap of alae of parasphenoid and median rami of pterygoids, and posterior deflection of parasphenoid alae; 33) relative bulk of pterygoid, length of anterior ramus and median ramus; 34) size, shape, and arrangement of occipital condyles; 35) development of mandibular odontoids; 36) shape of terminal phalanges; 37) size and shape of alary processes of hyoid plate; 38) cricoid cartilage divided ventrally or not; 39) patterns of insertion of *m. petrohyoideus anterior* and *m. sternohyoideus* on hyoid plate; 40) single or double slip of *m. depressor mandibulae*; 41) pupil shape—horizontal or vertical; 42) nuptial asperities on thumb and/or chest or not; type of vocal sac; 43) development of major body glands—parotoid, flank, lumbar, and inguinal; 44) tongue shape; 45) webbing of toes, shape of digital tips, development of tarsal folds, and presence of an outer metatarsal tubercle; 46) larval morphology—vent median or dextral, tooth rows, and development of labial papillae; 47) amplectic position; 48) egg deposition—foam nest, in water, or terrestrial situation; 49) snout-vent lengths of adults—abbreviated SVL; 50) tympanum visible, concealed, or absent; 51) any unique characters that are especially diagnostic of the genus.

Characters 1), 2), and 3) do not occur in any generic account and characters 5), 6), 14), 21), and 39) occur in only some generic accounts. Character 51) is used only when appropriate.

GENERA EXCLUDED FROM THE LEPTODACTYLIDAE

As a result of my reassessment of the variation of many characters used in the classification of the Leptodactylidae, three genera were found to belong to other families. *Geobatrachus* is removed from the Leptodactylidae primarily on the basis of discussions with Charles F. Walker concerning the systematic position of the genus; *Hylopsis*, long an enigmatic Neotropical frog genus, is a hylid and probably inseparable from *Hyla*; and *Rhinoderma* is excluded from the Leptodactylidae because it exhibits no close similarity to any of the 57 leptodactylid genera, but does exhibit some similarity to the endemic South American bufonid genera.

Geobatrachus Ruthven, 1915

Ruthven (1915) named *Geobatrachus walkeri* as a new genus and species of the Dendrobatidae. The species remains rare and is apparently endemic to the Santa Marta Mountains of Colombia. Noble (1931) considered *Geobatrachus* most closely allied to *Rhinoderma* and *Sminthillus*. Griffiths (1959) demonstrated that the species of *Sminthillus* are leptodactylids. He placed *Geobatrachus* and *Rhinoderma* in the Rhinodermatinae, a subfamily of the Leptodactylidae; the two genera were associated together because of their common pseudofirmisterny and edentulousness.

Dr. Charles F. Walker is currently engaged in a study of the relationships of *Geobatrachus* and does not consider it to be a leptodactylid genus. Teeth are present, the pectoral girdle is firmisternal, the sacral diapophyses rounded, the tarsal bones fused, and the anterior zonal elements of the pectoral girdle are greatly reduced or possibly absent. *Geobatrachus* is apparently a microhylid genus.

Hylopsis Werner, 1894

Werner (1894) named *Hylopsis platycephalus* as a new genus and species of the Cystignathidae. The type-locality is "South America." Werner's meager description of the holotype does not provide many clues as to its relationships but the following data are of significance in determining the status of *Hylopsis platycephalus*: pectoral girdle arciferal (inferred from the family assignment; Werner must have examined the pectoral girdle because he comments on the omosternum), omosternum cartilaginous (therefore present), pupil horizontal, large digital pads on hands and feet, fingers one-half webbed, and toes fully webbed.

The webbing pattern described by Werner is unique if *Hylopsis* is a leptodactylid; no leptodactylid now known has webbing between the fingers, and very few species have fully webbed feet. The webbing pattern is not unique in the Centrolenidae, Hylidae, or Pseudidae. Pseudids do not have digital pads whereas most centrolenids and hylids do. *Centrolene, Centrolenella, Hyla* (part), *Osteocephalus, Phrynohyas, Smilisca,* and *Sphaenorhynchus* have webbing patterns that are like that described for *Hylopsis*. All have horizontal pupils, but *Centrolene* and *Centrolenella* lack an omosternum. Werner reported the prevomerine teeth to be absent but did not give the size or sex of the unique holotype. If prevomerine tooth patches were absent and the specimen was half grown or an adult, then it is unlikely that *Hylopsis* could be associated with *Osteocephalus, Phrynohyas,* or *Smilisca*. Werner's description of the holotype suggests that the frog had a very different snout shape from that of *Sphaenorhynchus*. *Hylopsis* cannot be distinguished from *Hyla*, although this could be an artifact of Werner's description. If the genus is a bufonoid genus, then it must be close to or identical with *Hyla* (assuming Werner correctly presented the characters of the holotype).

Rhinoderma Duméril and Bibron, 1841

Rhinoderma was often placed in its own family or subfamily by pre-Noble systematists. Mivart (1869) and Boulenger (1882) placed it in the Engystomatidae. Noble (1931) argued that it was a brachycephalid—a heterogeneous Neotropical family group of derived bufonids. Davis (1935) and Griffiths (1954) argued that if the three brachycephalid subfamilies recognized by Noble were independently evolved from bufonids, then the Atelopodinae, Dendrobatinae, and Rhinodermatinae were families of frogs, not subfamilies.

Griffiths (1959) studied the Brachycephalidae and placed the included genera in four families: Atelopodidae *(Atelopus* and *Brachycephalus),* Bufonidae *(Cacophryne, Dendrophryniscus, Didynamipus,* and *Oreophrynella),* Leptodac-

tylidae *(Geobatrachus, Noblella, Rhinoderma,* and *Sminthillus),* and Ranidae *(Dendrobates, Phyllobates,* and *Prostherapis).* The three ranid genera were placed in the subfamily Dendrobatinae. The leptodactylid genera were placed in the Rhinodermatinae *(Geobatrachus* and *Rhinoderma)* and *Sminthillus* divided into three genera—*Euparkerella, Noblella,* and *Sminthillus,* which were all considered very closely related to *Eleutherodactylus.*

The breeding behavior of *Rhinoderma darwini* is unique among amphibians. Amplexus is axillary. Like many other frogs, the eggs are large (3-6 mm. in diameter), few in number (20-40), and pigmented. The eggs are laid in a sheltered terrestrial situation and are guarded by the male. After hatching, the larvae complete their development in the hypertrophied vocal sacs of the male. The mouthparts are modified; the tooth rows are 1/2 and a beak is present; the labial papillae are interrupted anteriorly, and the vent is median.

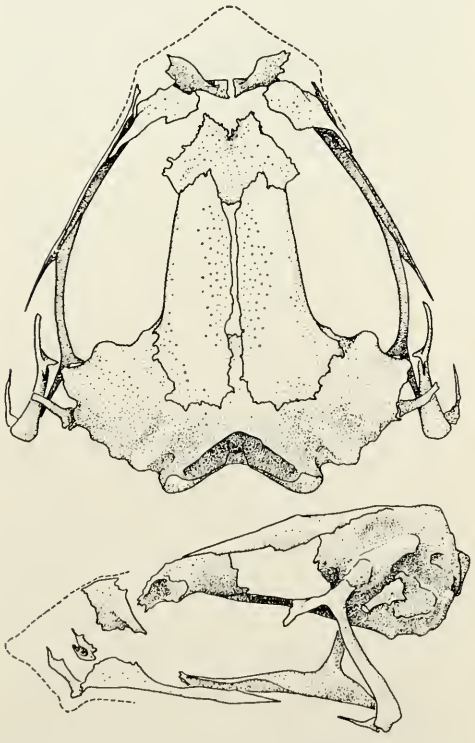

FIGURE 47. Dorsal and lateral views of the skull of *Rhinoderma darwini* (KU 68685, × 5.5). The anterior outline of the head is indicated by the dashed lines.

The skull of *Rhinoderma* is not heavily ossified (Fig. 47) except posteriorly. The occipital condyles are broad and close together and the cervical cotylar arrangement is type II. Teeth are lacking, the palatines and prevomers are lacking, the maxillary arch is incomplete, but the quadratojugal is present. The columella is present, the squamosal-maxillary angle is about 55°, and no otic plate is developed on the squamosal. The *m. depressor mandibulae* consists of the *pars tympanicus* only.

There are eight presacral vertebrae, all procoelus, and the cervical and second vertebrae are fused. The sacral diapophyses are broadly dilated, and the sacrum articulates with the coccyx by a bicondylar articulation. The pectoral girdle is pseudofirmisternal with free epicoracoidal horns and an omosternum and sternum are present and cartilaginous. The organ of Bidder is lacking. The terminal phalanges are knobbed. *Rhinoderma* lacks outer metatarsal tubercles.

Rhinoderma is clearly not related to the Dendrobatidae, as claimed by Cei (1962a), nor is it closely related to any other Neotropical group. It differs least from the endemic South American Bufonidae (several genera referred to the Atelopodidae or Bufonidae by various authors), but is clearly not a bufonid, because it lacks an otic plate on the squamosal, organ of Bidder, outer metatarsal tubercle, and has a well developed omosternum. The family Leptodactylidae is sufficiently loosely defined that the inclusion of *Rhinoderma* would not appreciably expand the family definition. If *Rhinoderma* is included in the Leptodactylidae, I would recognize it as the sole member of a subfamily. However, I anticipate that when a more thorough study of the Neotropical bufonids is made, the differences between *Rhino-*

derma and the Bufonidae will be in part demonstrated to be corollaries of the reduction in ossification in *Rhinoderma*. I prefer to recognize the Rhinodermatidae for this enigmatic Chilean genus and define the family as follows: bufonoid frogs with a pseudofirmisternal pectoral girdle, cartilaginous pre-zonal and post-zonal elements, lacking an organ of Bidder, palatines, prevomers, teeth, an otic plate on the squamosal, having broadly dilated sacral diapophyses, and a unique life history among frogs—tadpoles develop in the male vocal sacs.

KEYS TO THE GENERA OF LEPTODACTYLID FROGS

The purpose of a key should ultimately be for rapid and accurate identification of a specimen, regardless of what information accompanies it. Keys are especially useful in the identification by non-herpetologists of a specimen with no hint of its provenance. It is very difficult to prepare an effective key to a group of organisms when one places as a primary limitation that the characters used in that key will be characters that are readily accessible and/or superficial. In the family Leptodactylidae, as in most other groups, the members on different continents have undergone parallel modifications in adapting to their environment or to a particular mode of life. Therefore it is almost impossible to write a key, based on external (or superficially available internal) characters, to the Leptodactylidae on a world-wide level. Thus the following keys are 1) a key to the African and Australian genera and 2) a key to the African and American genera. *Heleophryne*, the sole African genus, has been included in both keys in an attempt to make the keys more cosmopolitan.

As superficial characters I include several characters readily visible once the skin in the tympanic region has been reflected; the presence or absence of a tympanic membrane can be observed as can the nature of the *musculus depressor mandibulae*. Most of the other characters used are those that traditionally have been used in keys.

Key to African and Australo-Papuan Leptodactylids

Two subfamilies of leptodactylids occur in Australia and are not readily separated by any "key" external character. Osteologically, they separate readily, but since my intent in preparing the keys was for utility in identifying preserved specimens, I have avoided using all but easily accessible osteological characters. All cycloranines possess prevomerine dentigerous processes and these processes are absent in all myobatrachines except for some of the species of *Crinia*. Outer metatarsal tubercles are absent in almost all cycloranines and present in all myobatrachines except some *Crinia* and *Taudactylus*. With the exception of the microcephalic *Myobatrachus*, all myobatrachines are very much smaller than any of the cycloranine leptodactylids. Absolute size however is a very poor key character.

1. *M. depressor mandibulae* in a single slip *(par tympanicus)* 2
   M. depressor mandibulae in two slips 4
2. Tympanic annulus absent ..... *Pseudophryne*
   Tympanic annulus present 3
3. Large parotoid glands present ..... *Philoria*
   Parotoid glands absent ..... *Crinia*
4. Prevomerine teeth absent 5
   Prevomerine teeth present 9
5. Outer metatarsal tubercle present 6
   Outer metatarsal tubercle absent ..... *Taudactylus*
6. Anal flap present; parotoid and flank glands present; pupil vertical in life ..... *Uperoleia*

Anal flap absent; parotoid glands absent or poorly defined; flank glands absent; pupil horizontal 7

7. Toes webbed ..... *Glauertia*
Toes devoid of webbing 8

8. Head minute compared to body ..... *Myobatrachus*
Head of normal proportions ..... *Metacrinia*

9. Maxillary teeth absent ..... *Notaden*
Maxillary teeth present 10

10. Prevomerine dentigerous processes between choanae 11
Prevomerine dentigerous processes posterior to choanae 14

11. First finger opposable to others ..... *Cyclorana*
First fiinger not opposable to others 12

12. Outer metatarsal separated by web ..... *Mixophyes*
Outer metatarsals united 13

13. Males with diffuse nuptial pads; toes one-third to fully webbed ..... *Neobatrachus*
Males with or without nuptial spines, no nuptial pads; toes one-fourth or less webbed ..... *Heleioporus*

14. Toes more than two-thirds webbed ..... *Heleophryne*
Toes less than one-third webbed 15

15. Tympanum clearly visible externally ..... *Lechriodus*
Tympanum partially or completely concealed 16

16. Prominent odontoids on lower jaw; diastema in tooth row on maxilla ..... *Adelotus*
No odontoids on mandible or diastema in maxillary tooth row 17

17. Fingers short, first shorter than second ..... *Kyarranus*
Fingers longer, first as long as or longer than second ..... *Limnodynastes*

Key to African and Neotropical Leptodactylids[5]

The following key is much less definitive than the former because several leptodactylid genera cannot be separated solely upon the basis of external characters. For example, the genera *Eupsophus* and *Niceforonia* cannot be separated on external characters but are readily separated once the nature of the occipital condylar-cervical articulation is known. I consider these two genera to belong to different tribes of the Telmatobiinae. In the later couplets in the key I have resorted to more and more osteological features—for the most part these are discernible with the aid of a thin probing needle and the figures of the skulls for reference.

The genera *Paratelmatobius* and *Pseudopaludicola* will key out in two sections of the key since the nature of the sternal style in *Pseudopaludicola* is difficult to assess from the examination of preserved material and because the osseous plate in *Paratelmatobius* is not a style.

As will be apparent, the genera *Eupsophus* and *Niceforonia* key out together three times in the following key (couplets 32, 34, and 42) and are never separated. Separation of these two genera on external characters is effectively impossible unless one has a breeding male (*Eupsophus* has nuptial asperities on the

[5] *Insuetophrynus* can be readily separated from all Neotropical leptodactylids as Barrio (1970) pointed out on the basis of the pectoral architecture. Presumably, the quadratojugal bone is present, and *Insuetophrynus* would key out at couplet 32 as "*Eupsophus* (part) and *Niceforonia* (part)." Inspection of the pectoral girdle will provide evidence for separating *Insuetophrynus*, because the former two genera have arciferal girdles in contrast to the pseudofirmisternal girdle of *Insuetophrynus*.

thumb whereas *Niceforonia* does not). *Eleutherodactylus* and *Syrrhophus* key out together (couplet 22). Most species may be separated by the presence of numerous supernumerary plantar tubercles in *Syrrhophus* and the absence of such tubercles in *Eleutherodactylus*. Some species of the Beta division of *Eleutherodactylus* have as many supernumerary tubercles as do *Syrrhophus* or more.

1. Cranial bones involved in dermostosis 2

   Cranial bones not involved in dermostosis 4

2. Toes fully webbed ..... *Caudiverbera*

   Toes less than two-thirds webbed 3

3. Pupil horizontal; outer metatarsal tubercle absent ..... *Ceratophrys*

   Pupil vertical; outer metatarsal tubercle present ..... *Lepidobatrachus*

4. Pupil vertical 5

   Pupil horizontal 9

5. Sternum a broad cartilaginous (sometimes calcified) plate 6

   Sternum bearing a distinct bony or calcified style 8

6. Toes fully webbed 7

   Toes free of webbing ..... *Hylorina*

7. Parotoid gland present; digital tips simple ..... *Telmatobufo*

   Parotoid gland absent; digital tips pad-like ..... *Heleophryne*

8. Toes fully webbed ..... *Hydrolaetare*

   Toes free or basally webbed ..... *Limnomedusa*

9. Sternum with a distinct bony or calcified style 10

   Sternum a cartilaginous, calcified, or osseous plate 17

10. Quadratojugal bone absent 11

    Quadratojugal bone present 12

11. Antebrachial tubercles present ..... *Pseudopaludicola*

    Antebrachial tubercles absent ..... *Pleurodema*

12. Prevomerine teeth absent ..... *Physalaemus*

    Prevomerine teeth present, on well defined processes 13

13. Eyelid bearing fleshy tubercles ..... *Edalorhina*

    Eyelid without fleshy tubercles 14

14. Sternal element style shaped 15

    Sternal element irregular in outline, plate-like ..... *Paratelmatobius*

15. Sternal style bifurcate posteriorly ..... *Barycholos*

    Sternal style not bifurcate posteriorly 16

16. Terminal phalanges distinctly T-shaped; digital discs with circumferential groove ..... *Lithodytes*

    Terminal phalanges knobbed or weakly T-shaped; no circumferential groove on digital discs ..... *Leptodactylus*

17. Dorsal surface of each digital pad bearing a pair of scute-like glands 18

    Dorsal surface of digital pad or tip without distinct glands 20

18. Quadratojugal absent or present only as a sliver-like bone; small frogs, adults less than 40 mm. SVL 19

    Quadratojugal massive; adults 50 to 110 mm. SVL ..... *Megaelosia*

19. Males with median subgular vocal sac; nuptial spines present; prevomerine teeth usually absent; quadratojugal bone absent ..... *Crossodactylus*

Males with paired lateral vocal sacs or none; nuptial spines absent; prevomerine teeth usually present; quadratojugal present ..... *Hylodes*

20. Tips of at least outer digits bearing transverse, terminal groove along edge of digital pad 21

    Tips of digits without terminal grooves 23

21. Maxillary arch toothless ..... *Sminthillus*

    Maxillary arch toothed 22

22. Lumbar gland present ..... *Tomodactylus*

    Lumbar gland absent ..... *Eleutherodactylus* and *Syrrhophus*

23. Terminal phalanges T-shaped or Y-shaped 24

    Terminal phalanges knobbed 26

24. Digital pads large, tympanum absent ..... *Crossodactylodes*

    Digital pads relatively narrow; tympanum visible externally 25

25. Quadratojugal bone present ..... *Thoropa*

    Quadratojugal bone absent ..... *Batrachyla*

26. Quadratojugal bone absent ..... *Pseudopaludicola*

    Quadratojugal bone present 27

27. Sternum an osseous plate ..... *Paratelmatobius*

    Sternum cartilaginous 28

28. Supernumerary plantar tubercles large, numerous 29

    Supernumerary plantar tubercles absent or small 30

29. Discoidal fold present ..... *Hylactophryne*

    Discoidal fold absent ..... *Ischnocnema*

30. Tympanic annulus absent 31

    Tympanic annulus visible externally or concealed beneath skin 33

31. Fingers short, especially fourth finger ..... *Euparkerella*

    Fingers of normal proportions to long 32

32. Toes fully webbed ..... *Batrachophrynus*

    Toes free to two-thirds webbed ..... *Eupsophus* (part) ..... and *Niceforonia* (part)

33. Tympanum visible externally 34

    Tympanum concealed beneath skin 35

34. Large frontoparietal crests present ..... *Amblyphrynus*

    No cranial crest ..... *Eupsophus* (part) ..... and *Niceforonia* (part)

35. Inner metatarsal tubercle spade-like elevated 36

    Inner metatarsal tubercle not elevated or spade-like 37

36. Large cranial crests present; parotid glands absent ..... *Proceratophrys* (part)

    Frontoparietal region flat or edge of frontoparietals slightly ridge-like; parotoid glands present or absent ..... *Odontophrynus*

37. Cranial crests present ..... *Proceratophrys* (part)

    Cranial crests absent 38

38. Metatarsal tubercles flat, sub-equal in size ..... *Holoaden*

    Inner metatarsal tubercle at least twice as large as outer 39

39. Outer metatarsal tubercle minute, less than one-fourth size of inner; toes webbed ..... *Telmatobius*

Outer metatarsal tubercle larger, about one-third to one-half size of inner; toes free or webbed; if webbed, outer tubercle one-half size of inner 40

40. Skin or dorsum uniformly pustular, toes free or webbed; large inguinal gland present ..... *Cycloramphus*

Skin or dorsum smooth or with scattered pustules; toes free of webbing; inguinal gland absent 41

41. Inner fingers and toes very short ..... *Scythrophrys*

Fingers and toes of normal length 42

42. Tongue free all around, anterior edge only slightly free; if appearing adherent anteriorly, axillary patagium present ..... *Zachaenus*

Tongue firmly adherent anteriorly; axillary patagium absent ..... *Eupsophus* (part) ..... and *Niceforonia* (part)

Leptodactylidae Berg, 1896 (1838)

Cystignathi Tschudi, 1838, Classification der Batrachier, p. 25, 37, 78. [Type-genus *Cystignathus* Wagler, 1830].

Leptodactylidae Berg, 1896, An. Mus. Buenos Aires, 5:161. [Type-genus *Leptodactylus* Fitzinger, 1826].

The subfamilial, tribal, and generic accounts follow. In the generic accounts, I have provided generic synonymies including all synonyms and permutations thereof and the manner of designation of the type-species; the diagnostic definition listing the states for the 50 characters scored for each genus; a statement of composition, and where appropriate, the most recent revisionary works on the group; a statement of distribution; and a section of remarks. In the remarks section, I have justified any new generic synonymies or partitionings. Brief remarks on the relationships of the genera are made in the remarks section.

Drawings of the skulls of all genera of leptodactylids are included with the exception of those genera known from so few specimens that the only available data are taken from stereo-radiographs. In genera having sufficient intrageneric variation (for example, *Cyclorana* and *Eleutherodactylus*), drawings of more than one species are included.

Cycloraninae Parker, 1940

Cycloraninae Parker, 1940:12.

In his monograph of the Australo-Papuan leptodactylids, Parker (1940) amply demonstrated the desirability of recognizing two subfamilies. My studies have further substantiated Parker's division of Noble's (1931) Criniinae into two subfamilies. Parker (1940) suggested that with additional study, it might be possible to demonstrate that there was a close relationship between some of the Cycloraninae and some Myobatrachinae. My studies have enhanced the differences, not mitigated them, and I consider that the two subfamilies possibly represent independently derived groups.

The following diagnostic statements are true for all members of the subfamily Cycloraninae: 1) sternum cartilaginous; 2) vertebral shield absent; 3) transverse processes of anterior presacral vertebrae not greatly expanded; 4) cervical cotylar arrangement type II; 6) cranial bones not dermostosed; 8) sacral diapophyses dilated; 14) maxillary arch complete; 20) frontoparietals not fused to proötics; 21) temporal arcade lacking; 27) columellae present; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 38) cricoid cartilage not divided ventrally; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on the lateral edges of hyoid plate; and 47) amplexus inguinal in known species. All species have dilated sacral diapophyses; Parker's (1940) statement to the contrary for *Mixophyes* is in error because his observation was made on a juvenile.

The primitive members of the subfamily exhibit some or all of the following characteristics: omosternum relatively large; cervical and second vertebrae fused; intervertebral discs free; transverse processes of posterior presacral vertebrae short and directed anteriorly; frontoparietal fontanelle lacking; carotid artery enclosed in a bony canal; outer metatarsal tubercle lacking; pupil vertical; eggs not deposited in a foam nest; aquatic tadpoles present; tadpole with median vent and 3/3 to 4/3 tooth rows.

Two tribes of the Cycloraninae are recognized herein. In the Cycloranini, the eggs are deposited in water without a foam nest, on land in moist situations, or in dry burrows with a foam nest. All species have aquatic tadpoles. Females lack spatulate fringes on the inner fingers (Fig. 48). The prevomerine dentigerous processes lie between, not posterior to, the choanae in all Cycloranini. In the Limnodynastini, the eggs are deposited in a foam nest floating on water or in a foam nest in moist terrestrial situations. All species except *Kyarranus* and *Philoria* have aquatic, feeding tadpoles. Development is direct in the montane *Kyarranus* and *Philoria*. Females of all Limnodynastini have spatulate fringes on the fingers (Fig. 48), which are used in the construction of the foam nest (Parker, 1940, Martin, 1968). The prevomerine dentigerous processes are situated posterior to the choanae in all Limnodynastini.

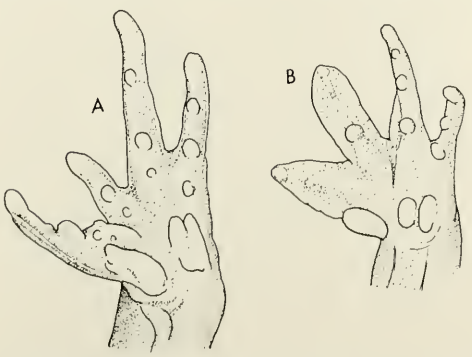

FIGURE 48. Palmar views of hands of adult females of (A) *Cyclorana australis* (KU 93545) and (B) *Limnodynastes peronii* (KU 93562). Both × 3.7.

Cycloranini Parker, 1940

Five genera are included in this tribe: *Cyclorana, Heleioporus, Mixophyes, Neobatrachus,* and *Notaden. Heleioporus* lays its eggs in dry burrows in a foam nest (Lee, 1966, Martin, 1968), but the other genera lay their eggs in water or in moist terrestrial sites (Martin, 1968).

Cyclorana Steindachner, 1867

(Figs. 49-50)

Chiroleptes Günther, 1859, Cat. Bat. Sal. British Mus., p. 34 [Type-species by monotypy, *Chiroleptes australis* (Gray), 1842; preoccupied by *Chiroleptes* Kirby, 1837 (Insecta: *Hemiptera*)].

Cyclorana Steindachner, 1867, Reise Novara, Amph., p. 29 [Type-species by monotypy, *Cyclorana novaehollandiae* Steindachner, 1867].

Phractops Peters, 1867, Mtber. k. Preuss. Akad. Wiss., Berlin, 1867:30 [Type-species by monotypy, *Phractops alutaceus* Peters, 1867.].

Mitrolysis Cope, 1889, Bull. U.S. Natl. Mus., 34:312 [Type-species by monotypy, *Chiroleptes albopunctatus* Günther, 1867].

Cheiroleptes Spencer, 1901, Proc. Roy. Soc. Victoria (2) 13:176 [Replacement name for *Chiroleptes* Günther, 1859 (preoccupied); hence taking the same type-species].

Diagnostic definition.—5) cervical and second vertebrae free; 7) omosternum present, moderate in size; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, relatively wide at base; 11) palatal shelf of premaxilla broad, deeply incised; 12) facial lobe of maxilla deep, weakly exostosed in *albopunctatus* and more so in *australis*; 13) palatal shelf of maxilla moderate in width, expanded posteriorly into a pterygoid process; 15) nasals separated medially, relatively small, exostosed in *australis*; 16) nasals in broad contact with maxillae, not in contact with pterygoids; 17) nasals separated from frontoparietals; 18) frontoparietal fontanelle

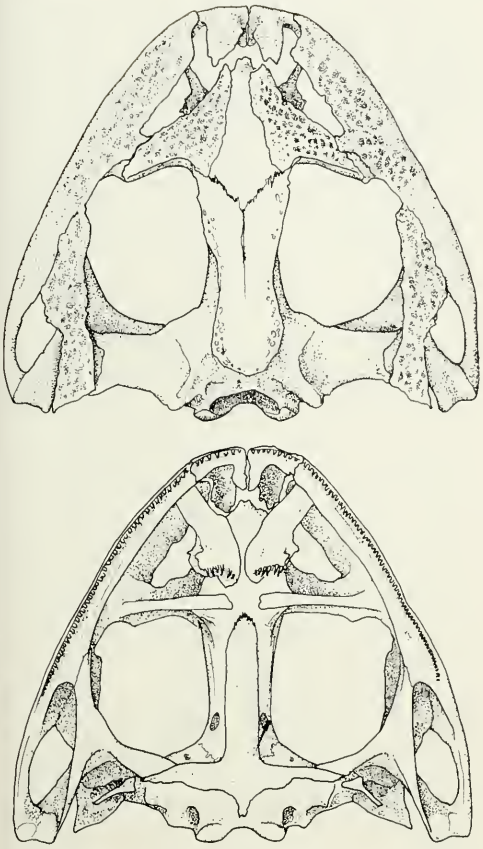

FIGURE 49. Dorsal and ventral views of the skull of *Cyclorana australis* (KU 93550, × 2.5).

lacking; 19) lateral edges of frontoparietals exostosed in *australis*, not ornamented in other species; 22) epiotic eminences prominent; 23) cristae paroticae long and relatively broad; carotid artery not enclosed in a bony canal; 24) zygomatic ramus of squamosal in broad articular contact with maxilla in *australis* and extensively sculptured; in tenuous contact with maxilla in *alboguttatus* and not ornamented; elongate but widely separated from maxilla in other species; 25) otic ramus of squamosal long, developed into small otic plate; in *australis*, otic plate is proportionately larger than that in other species and otic ramus is large and sculptured; 26) squamosal-maxillary angle 26-35°; 28) prevomers large, entire, toothed, narrowly separately medially; 29) palatines large, deep, bearing odontoid ridge in *australis*; 30) sphenethmoid entire, extending anterior beneath nasals; 31) anterior ramus of parasphenoid narrow, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped by median rami of pterygoids; 33) pterygoids moderate in size, no ventral flange, anterior rami in long contact with maxillae, not reaching palatines; 34) occipital condyles moderate sized, not stalked, narrowly separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median subgular vocal sac, nuptial asperities on thumb; 43) body lacking glands; 44)

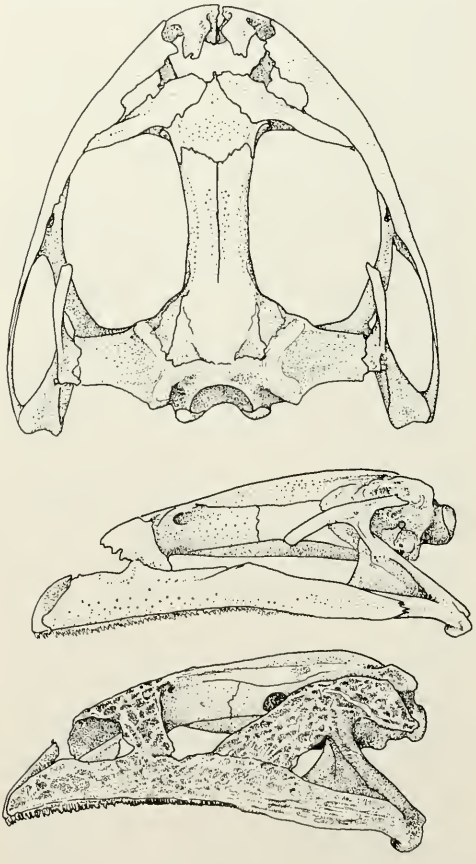

FIGURE 50. (Top) dorsal, (middle) lateral views of the skull of *Cyclorana dahli* (UMMZ 65250); and (bottom) lateral view of skull of *C. australis* (KU 93550). All × 2.5.

tongue large, free posteriorly; 45) toes webbed at base to fully webbed; outer metatarsal tubercle absent except in *inermis*; digital tips narrow; first finger longer than second; 46) larvae with median or dextral vent, 2/3 tooth rows, labial papillae interrupted anteriorly; 47) amplexus inguinal; 48) eggs laid in gelatinous masses in temporary ponds; 49) males 35-90, females 35-100 mm. SVL; 50) tympanum visible externally; 51) thumb opposable.

Composition.—Parker (1940) recognized seven species *(alboguttatus, australis, brevipes, cultripes, dahli, inermis,* and *platycephalus).* One other species *(slevini)* has been described since.

Distribution.—Australia except on the western coast and interior. The genus does not occur on New Guinea or Tasmania.

Remarks.—The generic synonymy of *Cyclorana* has been stable since 1940. The status of the nominal species of the genus is seriously in need of review. *Cyclorana* is a generalized genus of Cycloraninae. Osteologically, it is least different from *Lechriodus* and *Mixophyes,* but it has no close relationship with either of these genera.

The variation in the skulls of this genus is striking. *Cyclorana alboguttata* is intermediate between the heavily exostosed *australis* and the other species of the genus. The only other leptodactylid genus with comparable variation in the skull bones is *Eleutherodactylus.*

Heleioporus Gray, 1841

(Figs. 51-52)

Heleioporus Gray, 1841, Ann. Mag. Nat. Hist., (1)7:91 [Type-species by monotypy, *Heleioporus albopunctatus* Gray, 1841].

Helioporus Gray, in Grey, 1841, J. Exped. Cent. Australia, 2:447 [Emendation of *Heleioporus* Gray, 1841].

Perialia Gray, in Eyre, 1845, J. Exped. Cent. Australia, 1:406 [Type-species by monotypy, *Perialia eyeri* Gray, 1845].

Philocryphus Fletcher, 1894, Proc. Linn. Soc. New South Wales, (2)8:233 [Type-species by monotypy, *Philocryphus flavoguttatus* Fletcher, 1894].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum present, small; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla relatively narrow, moderately long palatal process; 12) facial lobe of maxilla of moderate depth, not exostosed; 13) palatal shelf of maxilla relatively narrow, pterygoid process present; 15) nasals small, short, very wide, separated medially; 16) nasals in broad contact with maxillae, separated from pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle moderate in size; 19) frontoparietals not ornamented; 22) epiotic eminences prominent posteriorly; 23) cristae paroticae long and narrow; carotid artery enclosed in a bony canal, roofed over; 24) zygomatic ramus of

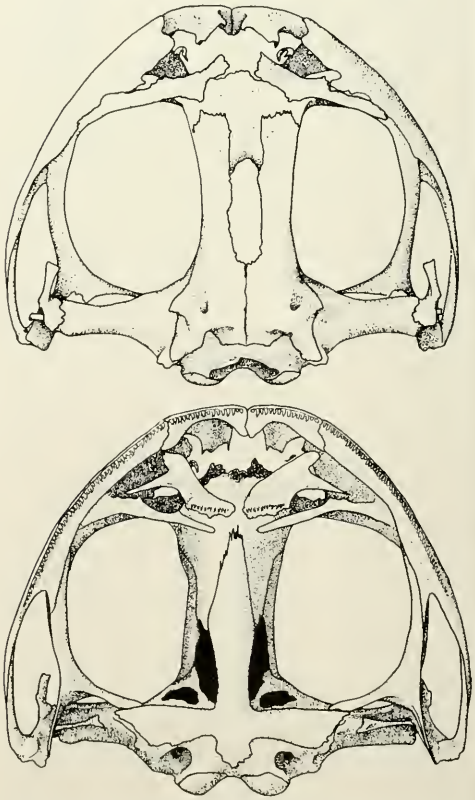

FIGURE 51. Dorsal and ventral views of the skull of *Heleioporus eyeri* (UMMZ 124504, × 6).

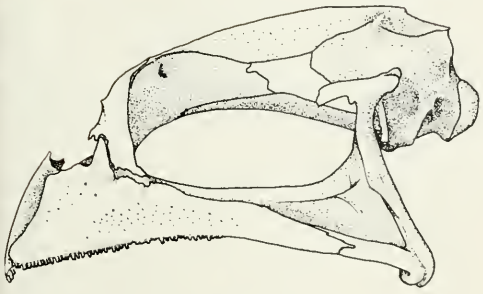

FIGURE 52. Lateral view of skull of *Heleioporus eyeri* (UMMZ 124504, × 6).

squamosal short, slightly longer than otic ramus; 25) otic ramus of squamosal developed into small otic plate; 26) squamosal-maxillary angle about 50°; 28) prevomers large, entire, toothed, narrowly separated medially; 29) palatines large, narrowly separated medially; 30) sphenethmoid entire, extending anteriorly beneath posterior half of nasals; 31) anterior ramus of parasphenoid narrow, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped by median rami of pterygoids; 33) pterygoids relatively slender, anterior rami in long contact with maxillae, reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil vertical; 42) males with large nuptial spines on thumb or not, never pad-like asperities; males with median, subgular vocal sac; 43) extensive parotoid glands present, small inguinal glands present; 44) tongue large, notched and free posteriorly; 45) feet basally webbed, outer metatarsal tubercle absent, inner metatarsal tubercle spade-like, tips of digits narrow, first finger longer than second; 46) larvae with median or dextral vent, 2/3 to 5/4 tooth rows, labial papillae broadly interrupted anteriorly; 47) amplexus inguinal; 48) eggs laid in foam nest in dry burrow, tadpoles emerge when nest is flooded; 49) males 38-95, females 41-95 mm. SVL; smallest species is *psammophilus*, largest is *australiacus*; 50) tympanum visible externally.

Composition.—Lee (1966) recognized six species (*albopunctatus, australiacus, barycragus, eyeri, inornatus,* and *psammophilus).*

Distribution.—Southeastern and southwestern Australia.

Remarks.—Parker (1940) did not differentiate the genera *Heleioporus* and *Neobatrachus.* Main, Lee, and Littlejohn (1958) considered the ethological and morphological differences between the groups ample for generic distinction. Moore (1961) and Lee (1966) concurred in this opinion; I consider the differences in the sizes of the transverse processes of the presacral vertebrae additional support for the continued separation of these genera. The two genera are unquestionably related but are not so similar that their combination would result in a clarification of relationships. *Neobatrachus* is more closely allied to a third related genus, *Notaden.*

Mixophyes Günther, 1864

(Figs. 53-54)

Mixophyes Günther, 1864, Proc. Zool. Soc. London, p. 46 [Type-species by monotypy, *Mixophyes fasciolatus* Günther, 1864].

Diagnostic definition.—5) cervical and second vertebrae free; 7) omosternum present, relatively large; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla narrow, palatal process elongate; 12) facial lobe of maxilla deep with a slight squamosal processes, not exostosed; 13) palatal shelf of maxilla very narrow, no pterygoid process; 15) nasals large, in median contact anteriorly, separated posteriorly, exposing sphenethmoid; 16) nasals in contact with maxillae, not in contact with pterygoids; 17) nasals in tenuous contact with frontoparietals; 18) frontoparietal fontanelle absent; 19) frontoparietals not ornamented; 22) epiotic eminences prominent; 23) cristae paroticae long and narrow; carotid artery enclosed in a complete bony canal; 24)

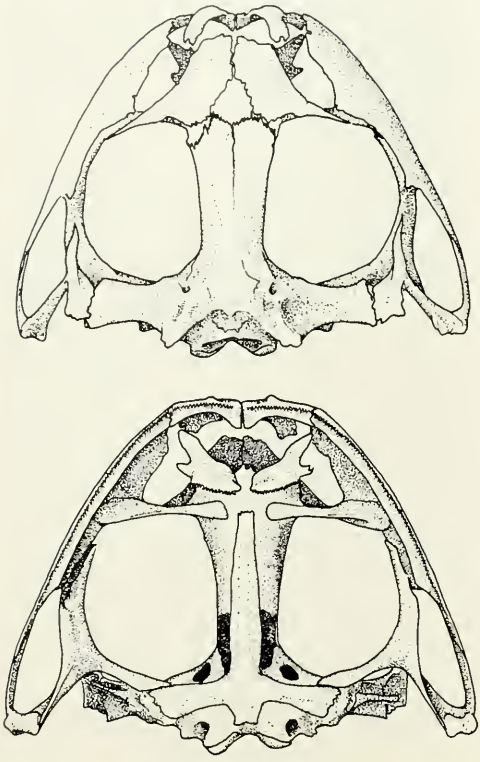

FIGURE 53. Dorsal and ventral views of skull of *Mixophyes fasciolatus* (KU 56627, × 3.5).

zygomatic ramus of squamosal elongate, tendon contacting squamosal process of maxilla; 25) otic ramus of squamosal long, developed medially into otic plate; 26) squamosal-maxillary angle 45-50°; 28) prevomers small, entire, toothed, separated medially; 29) palatines thin, separated medially, bearing odontoid ridges; 30) sphenethmoid entire, extending anteriorly to anterior edge of nasals; 31) anterior ramus of parasphenoid narrow, not keeled; 32) parasphenoid alae deflected posteriorly, overlapped laterally by median rami of pterygoids; 33) pterygoids large, anterior rami in long contact with maxillae, nearly reaching palatines and nasals; 34) occipital condyles moderate sized, not stalked, separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil vertical; 42) males with median subgular vocal sac, nuptial asperities on thumb; 43) body lacking glands; 44) tongue large, rounded, only posterior edge free; 45) toes two-thirds webbed, outer metatarsal tubercle absent, inner metatarsal tubercle not spade-like, tips of digits narrow; 46) larvae with dextral vent, 6/3 tooth rows, labial papillae not interrupted anteriorly; 47) amplexus inguinal; 48) eggs laid in terrestrial situations and hatch upon flooding; 49) males and females 50-100 mm. SVL; 50) tympanum visible externally.

Composition.—Only one species is now recognized, but it is apparently a composite of two (Moore, 1961, Littlejohn, 1968).

Distribution.—Mountains and coastal areas of eastern Australia.

Remarks.—*Mixophyes* has been recognized as a distinctive genus since its discovery. This distinction was based in part on misconceptions. Boulenger (1882) reported the sacral diapophyses as rounded; Parker (1940) agreed. Hecht (1960) reported the sacral diapophyses were dilated. The specimens I have examined all have dilated sacral diapophyses. Fletcher (1889) stated that *Mixophyes* exhibits axillary amplexus. Littlejohn (pers. comm.) informs me that the amplectic pattern is inguinal, as in all other Australo-Papuan leptodactylids.

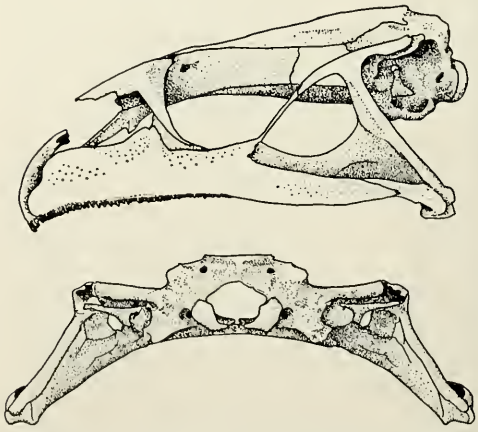

FIGURE 54. Lateral and occipital views of skull of *Mixophyes fasciolatus* (KU 56627, × 5.5).

Neobatrachus Peters, 1863
(Figs. 55-56)

Neobatrachus Peters, 1863, Mtber. k. Preuss. Akad. Wiss., Berlin, 1863:234 [Type-species by monotypy, *Neobatrachus pictus* Peters, 1863].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum minute; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae long, directed posterodorsally, relatively wide at base; 11) palatal shelf of premaxilla narrow, palatal process long; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla narrow, no pterygoid process; 15) nasals small, separated medially; 16) nasals in contact with maxillae, not with pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle moderate in size; 19) frontoparietals not ornamented; 22) epiotic eminences prominent; 23) cristae parotidae long and narrow; carotid artery lies in a deep groove, exposed dorsally; 24) zygomatic ramus of squamosal minute; 25) otic ramus of squamosal very small, developed medially into a small otic plate; 26) squamosal-maxillary angle 50-55°; 28) prevomers of moderate size, entire, toothed, narrowly separated medially; 29) palatines thin, widely separated medially; 30) sphenethmoid entire, extending anteriorly beneath nasals; 31) anterior ramus of parasphenoid narrow, weakly keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively large, anterior rami in long contact with maxillae, not reaching palatines; 34) occipital condyles relatively small, not stalked, narrowly separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil vertical; 42) males with median subgular vocal sac; nuptial pad (callosities) on thumb and second finger; 43) body lacking glands; 44) tongue large, round, free behind; 45) toes one-fourth to fully webbed, outer

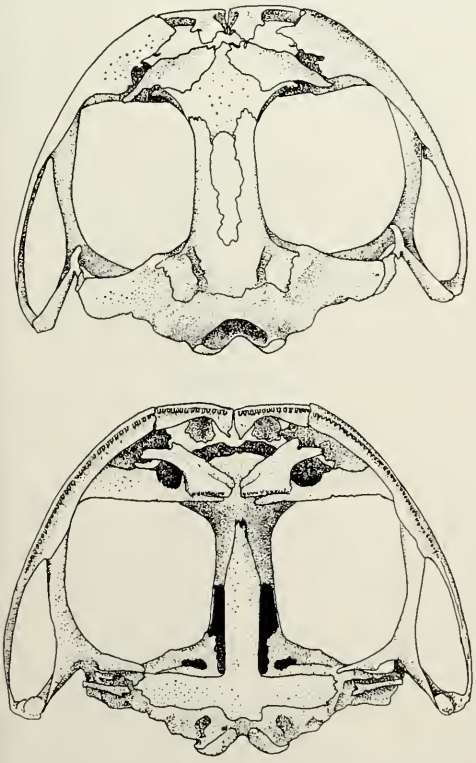

FIGURE 55. Dorsal and ventral views of skull of *Neobatrachus pictus* (FMNH 97281, × 3).

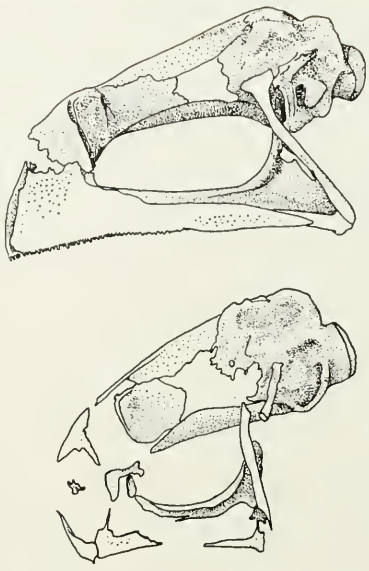

FIGURE 56. Lateral views of the skulls of *Neobatrachus pictus* (FMNH 97281, top) and *Notaden nichollsi* (KU 93582, bottom). Both × 3.

metatarsal tubercle absent, inner metatarsal tubercle spade-like, tips of digits narrow, first finger longer than second; 46) larvae with dextral vent, 3/3 tooth rows, labial papillae interrupted anteriorly; 47) amplexus inguinal; 48) eggs deposited in long strings in slow moving streams and temporary ponds; 49) adults not exceeding 50 mm. SVL; 50) tympanum indistinct externally, concealed beneath skin.

Composition.—Five species *(centralis, pelobatoides, pictus, sutor,* and *wilsmorei)* are presently recognized, although no one has reviewed the group since Parker (1940).

Distribution.—Mainland Australia except in northern West Australia and along the northern coast, where *Neobatrachus* is apparently replaced ecologically by its close relative, *Notaden.*

Remarks.—Main, Lee, and Littlejohn (1958) argued that the *Heleioporus pictus* group *(Neobatrachus)* should be afforded generic status since it differs ethologically from typical *Heleioporus.* Typical *Heleioporus* lays the eggs in burrows in a foam nest and when the burrow is flooded, the tadpoles emerge to complete their development like typical frogs. *Neobatrachus* lays long egg strings (like *Bufo*) in still or slowly moving water. The two groups also differ in the kind of nuptial excrescence (spines in *Heleioporus,* roughened pad in *Neobatrachus*), adult size (*Heleioporus* are larger frogs), and the shape of the sternum (bifurcate posteriorly in *Heleioporus*). The transverse processes of the posterior presacral vertebrae of the two genera differ in size (Fig. 30), and there is a slight difference in the sizes of the zygomatic and otic rami of the squamosals.

The separation of these two genera is based more on the so-called adaptive approach to genera than the morphological approach. Without the ethological data, I doubt if I would have adopted a different approach from that taken by Parker (1940).

Notaden Günther, 1873

(Figs. 56-57)

Notaden Günther, 1873, Ann. Mag. Nat. Hist., (4)11:349 [Type-species by monotypy, *Notaden bennetti* Günther, 1873].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum absent; 9) maxillary arch edentate; 10) alary processes of premaxillae elongate, directed dorsally, narrow at base; 11) palatal shelf of premaxilla narrow, palatal process relatively short; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla absent; 14) maxillary arch incomplete, maxilla not contacting quadratojugal or premaxilla, quadratojugal present; 15) nasals small and separated medially; 16) nasals not in contact with maxillae or pterygoids; 17) nasals in tenuous contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences prominent; 23) cristae paroticae short, stocky; carotid artery lies in a shallow groove exposed dorsally; 24-25) zygomatic and otic rami of squamosal lacking; 26) squamosal-maxil-

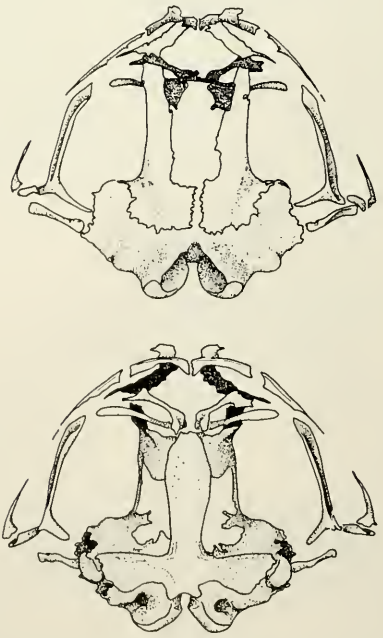

FIGURE 57. Dorsal and ventral views of skull of *Notaden nichollsi* (KU 93582, × 3).

lary angle about 80°; 28) prevomers moderately large, entire, toothed, separated medially; 29) palatines reduced in size, not contacting maxillae and widely separated medially; 30) sphenethmoid entire, small, not extending anteriorly to nasals; 31) anterior ramus of parasphenoid broad, short, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, not overlapped laterally by median rami of pterygoids; 33) pterygoids small, anterior rami in long contact with maxillae, usually contacting palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median subgular vocal sac; nuptial pad on thumb; 43) dorsum covered with at least two ill-defined glands, less discrete but more extensive than in *Heleioporus*; 44) tongue large, round, not free behind; 45) toes one-half to two-thirds webbed, outer metatarsal tubercle absent, inner metatarsal tubercle spade-like, tips of digits narrow, first finger about as long as second; 46) larvae with median vent, 3/3 tooth rows, labial papillae interrupted anteriorly; 47-48); 49) adults to 70 mm. SVL; 50) tympanum concealed.

Composition.—Hosmer (1962) recognized three species—*bennetti, melanoscaphus,* and *nichollsi.*

Distribution.—Northwestern, north-central, and southeastern Australia west of the dividing range.

Remarks.—*Notaden* has been recognized as distinct since its description chiefly because it lacks maxillary teeth. The loss of teeth reflects a general reduction in the amount of bone; in *Notaden,* the reduction is striking. The loss of the upper portions of the squamosals is unique in the family, as is the free floating maxilla. Because *Notaden* lives in an arid environment, Parker (1940) thought it might exhibit direct development. Slater and Main (1963) found tadpoles in ponds and suggested that development was rapid, but definitely was not abbreviated.

Notaden is closely related to *Heleioporus* and *Neobatrachus.* All have free intervertebral discs, fused cervical and second vertebrae, short transverse processes of the posterior presacral vertebrae, moderate to large frontoparietal fontanelles, deep skulls, and large, spade-like inner metatarsal tubercles. *Notaden* has a horizontal pupil and lacks maxillary teeth, whereas the other two genera have vertical pupils and have maxillary teeth. *Notaden* and *Heleioporus* have extensive glandular areas on the dorsum; *Neobatrachus* lacks glands. *Neobatrachus* and *Notaden* have nuptial pads, and *Heleioporus* has large spines on the thumb. The tadpoles of the three genera are similar and cannot be separated generically owing to the intrageneric variability in vent position and tooth rows in *Heleioporus.*

Limnodynastini New Tribe

Limnodynastine leptodactylids build a foam nest in which the eggs are deposited. The few observations that have been made indicate that the female uses the spatulate fringes on the inner fingers (Fig. 48) to build the nest. Development is direct in two of these genera *(Kyarranus* and *Philoria).*

Martin (1968) proposed an evolutionary course of terrestrial foam nest development. He cited Australo-Papuan genera where germane, but used Neotropical genera for certain stages of development. The foam nest is deposited in open water by some *Limnodynastes,* in water-filled burrows adjacent to open water in other *Limnodynastes,* in puddles adjacent to open water in *Leptodactylus pentadactylus,* in dry burrows which will later flood in *Heleioporus,* and in moist, terrestrial situations in *Kyarranus* and *Philoria.*

Adelotus Ogilby, 1907
(Figs. 58-59)

Cryptotis Günther, 1863, Ann. Mag. Nat. Hist., (3)11:27 [Type-species by monotypy, *Cryptotis brevis* Günther, 1863; preoccupied by *Cryptotis* Pomel, 1848 (Mammalia: Insectivora)].

Adelotus Ogilby, 1907, Proc. Roy. Soc. Queensland, 20:32 [Replacement name for *Cryptotis* Günther, 1863 (preoccupied); hence taking same type-species].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum present, moderate sized; 9) maxillary arch toothed, teeth elongate, pedicellate; distinct diastema in tooth row; 10) alary processes of premaxillae directed posterodorsally, elongate, relatively broad at base; 11) palatal shelf of premaxilla narrow with a moderately large palatal process and long process lying along maxilla; 12) facial lobe of maxilla deep; maxilla deep for entire length, not exostosed; 13) palatal shelf of maxilla narrow, pterygoid process well developed; 14) quadratojugal expanded; 15) nasals wide and short, small, separated medially; 16) nasals in contact with maxillae, not with pterygoids; 17) nasals widely separated from frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals not exostosed but bearing large sagittal crest; 22) epiotic eminences obsolete; 23) cristae paroticae short but relatively broad; carotid artery not enclosed in an open or closed canal; 24) zygomatic ramus of squamosal slender, of moderate length; 25) otic ramus of squamosal short, developed medially into prominent otic plate; 26) squamosal-maxillary angle about 45°; 28) prevomers toothed, entire, separated medially, dentigerous ramus greatly elongated; 29) palatines very broad, lacking odontoid ridge, separated medially; 30) sphenethmoid entire, relatively small, rounded anteriorly, not reaching nasals; 31) anterior ramus of parasphenoid broad, not keeled, anterior edge deeply serrated; 32) parasphenoid alae deflected posteriorly, short, overlapped laterally by median rami of pterygoids; 33) pterygoids relatively large, anterior rami in long contact with maxillae, nearly reaching palatines; 34) occipital condyles large, closely approximated medially; 35) mandible bearing elongate tusk (Fig. 15), longer in male than in female; 40) *m. depressor mandibulae* in two slips; 41) pupil hori-

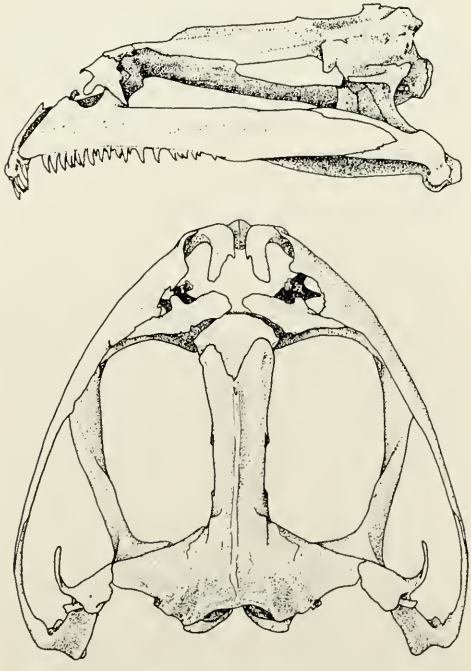

FIGURE 58. Lateral and dorsal views of the skull of *Adelotus brevis* (KU 56242, × 2.5).

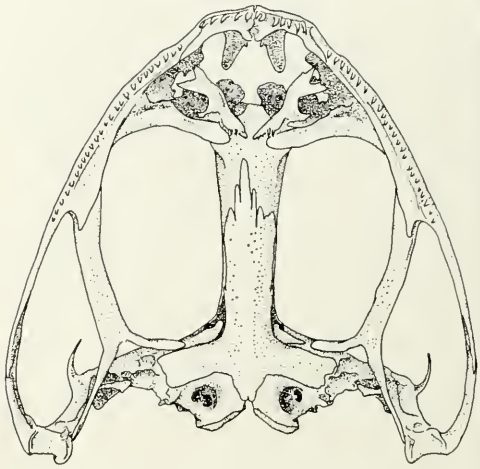

FIGURE 59. Ventral view of the skull of *Adelotus brevis* (KU 56242, × 2.5).

zontal; 42) males with median subgular vocal sac; no nuptial asperities on thumb; 43) body lacking glands; 44) tongue large, posterior edge free; 45) toes with basal webbing, outer metatarsal tubercle present, digital tips narrow, first finger as long as second; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae narrowly interrupted anteriorly; 47) amplexus inguinal; 48) eggs laid in foam nest in ponds or running water (streams); 49) males to 50 mm., females to 40 mm. SVL; 50) tympanum usually completely concealed.

Composition.—A single species, *A. brevis.*

Distribution.—Coastal southeastern Australia.

Remarks.—Since its discovery, the tusked frog has been recognized as generically distinct. The large mandibular tusks are characters *sui generis.* The species was originally named *Cryptotis brevis* but the generic name, *Cryptotis* Günther, 1863, is a junior homonym of *Cryptotis* Pomel, 1848, the generic name of some American shrews. *Adelotus* is not closely related to any other genus of the Limnodynastini, but is least different from *Limnodynastes.*

Lechriodus Boulenger, 1882
(Fig. 60)

Batrachopsis Boulenger, 1882, Cat. Batr. Sal. British Mus., p. 439 [Type-species by monotypy, *Asterophrys melanopyga* Doria, 1875; preoccupied by *Batrachopsis* Fitzinger, 1843 (Amphibia: Caudata)].

Lechriodus Boulenger, 1882, Cat. Batr. Grad. British Mus., p. 116 [Replacement name for *Batrachopsis* Boulenger, 1882 (preoccupied) and hence taking same type-species].

Phanerotis Boulenger, 1890, Proc. Linn. Soc. New South Wales, (2)5:594 [Type-species by monotypy, *Phanerotis fletcheri* Boulenger, 1890].

Diagnostic definition.—5) cervical and second vertebrae free; 7) omosternum present, moderate sized; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, wide at base; 11) palatal shelf of premaxilla moderate

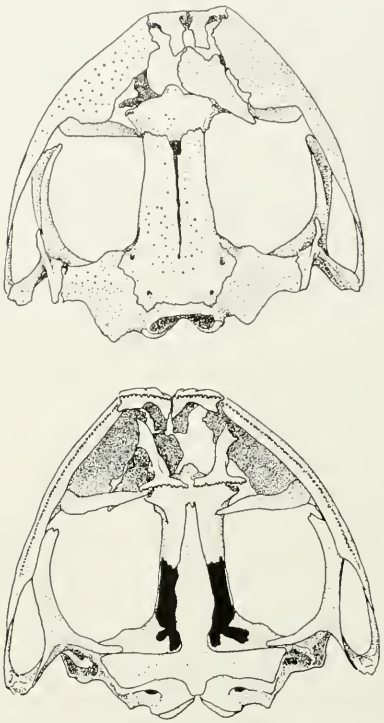

FIGURE 60. Dorsal and ventral views of skull of *Lechriodus fletcheri* (AMNH 59488, × 3).

in width, deeply incised; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla relatively narrow, small pterygoid process; 15) nasals moderate sized, apparently in median contact; 16) nasals in contact with maxillae, not with pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals not ornamented; 22) epiotic eminences poorly defined; 23) cristae paroticae long and relatively broad; carotid artery enclosed in long, roofed, bony canal; 24) zygomatic ramus of squamosal slightly shorter than otic ramus; 25) otic ramus of squamosal of moderate length, expanded medially into small otic plate; 26) squamosal-maxillary angle about 50°; 28) prevomers entire, toothed, large, dentigerous rami in tenuous median contact; 29) palatines large, narrowly separated medially; 30) sphenethmoid entire, extending anteriorly beneath posterior edge of nasals; 31) an-

terior ramus of parasphenoid narrow, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, overlapped laterally by median rami of pterygoids; 33) pterygoids relatively large, anterior rami in long contact with maxillae, nearly reaching palatines; 34) occipital condyles moderately large, not stalked, narrow separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median subgular vocal sac; nuptial asperities of many small spines on thumb; 43) body lacking glands; 44) tongue round, posterior edge free; 45) toes lack webbing, outer metatarsal tubercle absent, digital tips narrow, first finger as long as second; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 47) amplexus inguinal; 48) eggs laids in foam nest in temporary ponds and puddles; 49) males 40-70, females 40-96 mm. SVL; 50) tympanum visible externally.

Composition.—Parker (1940) recognized four species *(fletcheri, melanopygus, papuanus,* and *platyceps).* The species of this genus appear to be sorely in need of review.

Distribution.—Eastern New Guinea, the Aru Islands, and the eastern edge of Australia southward to New South Wales.

Remarks.—*Lechriodus* was long-thought to be the only Australo-Papuan pelobatid genus. Noble (1926a) demonstrated that *Lechriodus* was a leptodactylid (bufonid in his terminology). In many respects, *Lechriodus* is the most primitive genus of Limnodynastini—the skull is completely roofed, and the maxillary dentition is similar to that seen in the Cycloranini. In terms of breeding biology, it is only slightly more advanced than the generalized *Limnodynastes.* The firmly ankylosed intervertebral discs and the non-fusion of the cervical and second vertebrae possibly are advanced characters.

Limnodynastes Fitzinger, 1843
(Figs. 61-62)

Limnodynastes Fitzinger, 1843, Syst. Rept., 31 [Type-species by original designation, *Cystignathus peronii* Duméril and Bibron, 1841].

Wagleria Girard, 1853, Proc. Acad. Nat. Sci. Philadelphia, 6:421 [Type-species by monotypy, *Cystignathus peronii* Duméril and Bibron, 1841].

Platyplectrum Günther, 1863, Ann. Mag. Nat. Hist., (3)11:27 [Type-species by monotypy, *Platyplectrum marmoratum* Günther, 1863].

Platyplectron Peters, 1863, Mtber. k. Preuss. Akad. Wiss., Berlin, 1863:235 [Emendation of *Platyplectrum* Günther, 1863; hence taking same type-species].

Lymnodynastes Cope, 1865, Rev. Nat. Hist., 5:113 [Emendation of *Limnodynastes* Fitzinger, 1843; hence taking same type-species].

Opisthodon Steindachner, 1867, Reise Novara, Amph., p. 9 [Type-species by monotypy, *Opisthodon frauenfeldti* Steindachner, 1867].

Heliorana Steindachner, 1867, *Ibid.*, p. 32 [Type-species by monotypy, *Heliorana grayi* Steindachner, 1867].

Ranaster MaCleay, 1878, Proc. Linn. Soc. New South Wales, 2:135 [Type-species by monotypy, *Ranaster convexiusculus* MaCleay, 1878].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum present, moderately large; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, wide at base; 11) palatal shelf of premaxilla relatively narrow, palatal process present; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla narrow, pterygoid process small; 15) nasals relatively small and widely separated medially; 16) nasals in broad contact with maxillae, not contacting pterygoids; 17) nasals separated from frontoparietals; 18) frontoparietal fontanelle present, moderate-sized; 19) frontoparietals not ornamented; 22) epiotic eminences prominent; 23) cristae paroticae relatively short, stocky; carotid artery not enclosed in bony canal or groove; 24) zygomatic ramus of squamosal as long as otic ramus, widely separated from maxilla; 25) otic ramus of squamosal

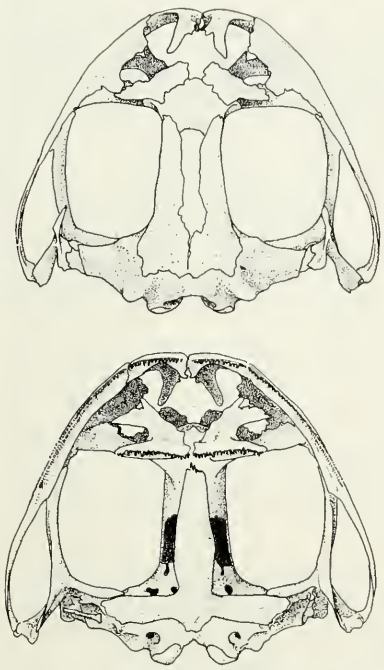

FIGURE 61. Dorsal and ventral views of skull of *Limnodynastes dorsalis* (KU 93553, × 2.2).

moderate length, developed medially into small otic plate; 26) squamosal-maxillary angle about 50°; 28) prevomers large, entire, toothed, narrowly separated medially; 29) palatines broad, narrowly separated medially; 30) sphenethmoid entire, extending anteriorly to center of nasals; 31) anterior ramus of parasphenoid of moderate width, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids slender and large, anterior rami in long contact with maxillae, not reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially in *dorsalis* group, moderately separated medially in *peronii* group; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median subgular vocal sac; males of *convexiusculus, dorsalis, ornatus, spenceri,* and *tasmaniensis* have nuptial pads on thumb, whereas males of *fletcheri, peronii, salmini,* and the Eidsvold *tasmaniensis* lack nuptial asperities; 43) tibial glands in *dorsalis,* other species lacking glands; 44) tongue large, slightly notched, free posteriorly; 45) toes lacking web to one-half webbed, inner metatarsal tubercle spade-like in the *dorsalis* group, normal in the *peronii* group, outer metatarsal tubercle absent in all species except *tasmaniensis,* digital tips narrow, first finger shorter than to longer than second; 46) larvae with median vent, 3/3 to 4/3 tooth rows, labial papillae broadly interrupted anteriorly; 47) amplexus inguinal; 48) eggs laid in foam nest floating in open water or in water-filled holes adjacent to the main body of water; 49) males 32-87, females 32-83 mm. SVL; 50) tympanum visible externally or indistinct.

Composition.—Parker (1940) recognized eight species—*convexiusculus, dorsalis, fletcheri, ornatus, peronii, salmini, spenceri,* and *tasmaniensis.* Moore (1961) suggested that *spenceri* was a subspecies of *ornatus*; he discussed a population of *tasmaniensis*-like frogs and considered them subspecifically or specifically distinct but did not name or otherwise treat them taxonomically. Littlejohn (1968) noted northern and southern call races of *tasmaniensis.* Parker (1940) recognized five subspecies of *dorsalis,* but Moore (1961) did not discuss their status; Littlejohn (1968) recognized the four that occur in southeastern Australia and Tasmania but stated that they hybridize (not intergrade) wherever their ranges meet thereby suggesting that the five are species. The nominal forms are *dorsalis, dumerili, grayi, insularis,* and *interioris.*

Distribution.—Australia and Tas-

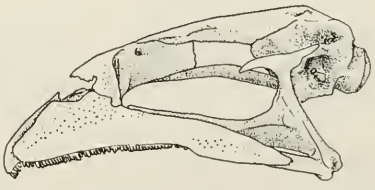

FIGURE 62. Lateral view of skull of *Limnodynastes dorsalis* (KU 93553, × 2).

mania; the genus is apparently absent from most of the western Eyrean subregion.

Remarks.—The two species-groups of *Limnodynastes* are readily separated. The *dorsalis* group *(dorsalis, ornatus,* and *spenceri)* is composed of medium sized, stocky frogs with large, spade-like inner metatarsal tubercles. The *peronii* group is composed of smaller species with a *Rana*-like habitus and "normal" inner metatarsal tubercle. Frogs of the *dorsalis* group are burrowers, whereas those of the *peronii* group seldom burrow. The data presently available are sufficient to assert that the genus *Limnodynastes* does not contain enough variability to justify recognition of subgenera.

Cope (1866) combined *Limnodynastes* with *Borborocaetes* (an emendation of *Borborocoetes* Bell; principally refers to *Eupsophus*). In an earlier paper Cope (1865) had considered them closely related but separable on the basis of the lateral extension of the prevomerine tooth rows. *Limnodynastes* and *Eupsophus* differ in many respects—principally characters with which Cope was not familiar. The breeding biology of the two is quite different, and the vertebral column of *Limnodynastes* does not resemble that of *Eupsophus*; both are relatively generalized leptodactylids. The superficial skull bones of the two are very similar. Among the most important characters in Cope's system were the separation of the prefrontals (=nasals) and the presence of a frontoparietal fontanelle—*Eupsophus* and *Limnodynastes* agree in these two characters.

Kyarranus Moore, 1958
(Fig. 63)

Kyarranus Moore, 1958, Amer. Mus. Novitates, 1919:1 [Type-species by original designation, *Kyarranus sphagnicolus* Moore, 1958 (=*Kyarranus sphagnicola*)].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum present, small; 9) maxillary arch

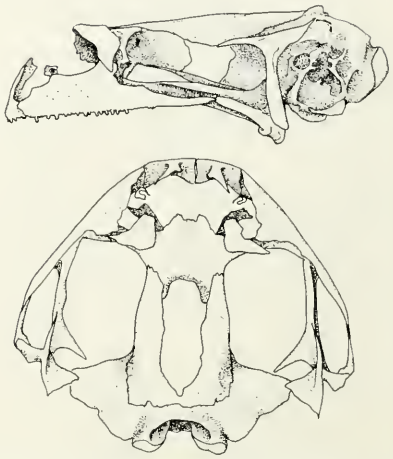

FIGURE 63. Lateral (× 2.6) and dorsal (× 2.3) views of the skull of *Kyarranus sphagnicola* (KU 110331).

toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed dorsally, relatively wide at base; 11) palatal shelf of premaxilla relatively narrow, palatal process large; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla of moderate width, pterygoid process small; 15) nasals small, widely separated medially; 16) nasals in contact with maxillae, not with pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae short and stocky; carotid artery enclosed in short, roofed, bony canal; 24) zygomatic ramus of squamosal relatively long, widely separated from maxilla; 25) otic ramus of squamosal slightly shorter than zygomatic ramus, expanded medially into moderately large otic plate; 26) squamosal-maxillary angle about 65°; 28) prevomers entire, toothed, widely separated; 29) palatines wide, narrowly separated medially; 30) sphenethmoid entire, extending anteriorly to anterior edge of nasals; 31) anterior ramus of parasphenoid broad, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, overlapped laterally by median rami of pterygoids;

33) pterygoids slender, anterior rami in long contact with maxillae, nearly reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with nuptial callosities on thumb; median, subgular vocal sac; 43) body lacking glands; 44) tongue large, notched posteriorly, posterior edge free; 45) toes free of webbing, outer metatarsal tubercle lacking, digital tips narrow, first finger shorter than second; 46) development direct; 47) amplexus inguinal; 48) eggs laid underground in sphagnum or loose earth in a foam nest; 49) males 21-35, females 30-34 mm. SVL; 50) tympanum concealed.

Composition.—Two species *(loveridgei* and *sphagnicola).*

Distribution.—The New England Range of eastern Australia and a dubious record from Warragul, Victoria (lowlands).

Remarks.—Parker (1940) named *loveridgei* as a species of *Philoria*; Moore (1958) reëxamined the holotype of *Philoria frosti* and concluded that *loveridgei* was generically different from *frosti.* He included *loveridgei* with a new species from the southern part of the New England Range in a new genus, *Kyarranus.* The principal differences between *Kyarranus* and *Limnodynastes,* according to Moore (1958, 1961), were in breeding biology—the former exhibits direct development and the latter has tadpoles. Littlejohn (1963) questioned the separation of *Kyarranus* and *Philoria* after he found that *Philoria* also exhibits direct development. The two genera differ in the development of the parotoid glands and in the arrangement of several skull bones. *Kyarranus* has a large frontoparietal fontanelle and widely separated nasals; in *Philoria,* the fontanelle is small and the nasals large and broadly in contact.

Philoria Spencer, 1901

(Fig. 64)

Philoria Spencer, 1901, Proc. Roy. Soc. Victoria, 13(2):176 [Type-species by monotypy, *Philoria frosti* Spencer, 1901].

Diagnostic definition.—5) cervical and second vertebrae fused; 7) omosternum present, small; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, wide at base; 11) palatal shelf of premaxilla of moderate width, palatal process small; 12) facial lobe of maxilla deep anteriorly, shallow posteriorly; 13) palatal shelf of maxilla of moderate width, large pterygoid process posteriorly; 15) nasals large, in broad median contact; 16) nasals not in contact with maxillae or pterygoids; 17) nasals in contact with frontoparietals; 18) frontoparietal fontanelle present, relatively small; 19) frontoparietals not ornamented; 22) epiotic eminences poorly defined; 23) cristae paroticae relatively short and stocky; carotid artery enclosed

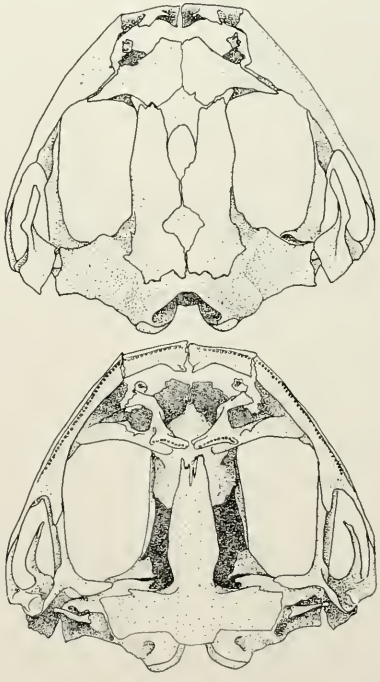

FIGURE 64. Dorsal and ventral views of skull of *Philoria frosti* (KU 50699, × 4).

in a short, complete, canal; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal long, large, expanded medially into very large otic plate; 26) squamosal-maxillary angle about 58°; 28) prevomers moderate-sized, entire, toothed, widely separated medially; 29); palatines large, widely separated medially; 30) sphenethmoid entire, large, extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid broad, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, slightly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively small, anterior rami in long contact with maxillae, not reaching palatines; 34) occipital condyles large, not stalked, separated medially; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in one slip—*pars tympanicus*; 41) pupil horizontal; 42) males with median subgular vocal sac but lacking nuptial asperities; 43) very large parotoid gland present; 44) tongue large, oval, free posteriorly; 45) toes free of webbing, outer metatarsal tubercle absent, inner of normal shape and size, first finger shorter than second; 46) development probably direct in nature; in laboratory-raised clutch, the tadpoles hatched but did not feed; had median vent, and mouth parts greatly reduced (Littlejohn, 1963); 47) amplexus inguinal; 48) eggs laid in foam nests in burrows and in holes dug in sphagnum; 49) males 41-46, females 47-51 mm. SVL; 50) tympanum concealed.

Composition.—Monotypic, *P. frosti.*

Distribution.—Known only from Mount Baw Baw, Victoria, Australia.

Remarks.—*Philoria* is related to *Kyarranus* and *Limnodynastes.* The three genera are readily distinguished on the basis of body glands and skeletons. *Kyarranus* and *Philoria* are superficially very similar in that their breeding biologies are identical, both are genera of stubby frogs with short fingers, and the tympani are concealed. The similarity, in part, is probably due to adaptation to montane environments because several Neotropical genera living in the Andes, bear superficial resemblance to these Australian frogs. *Kyarranus* and *Philoria* probably represent independent divergences from a *Limnodynastes*-like ancestor.

Myobatrachinae Schlegel, 1850

Myobatrachidae Schlegel, 1850:10.
Uperoliidae Günther, 1859a:39.
Criniae Cope, 1866:89.
Criniinae: Noble, 1931:496.
Myobatrachinae: Parker, 1940:64.

The Myobatrachinae, as presently conceived, are restricted in distribution to the Australo-Papuan Region. The following diagnostic statements are true for all members of the subfamily Myobatrachinae: 1) sternum cartilaginous; 2) vertebral shield absent; 3) transverse processes of anterior presacral vertebrae not greatly expanded; 4) cervical cotylar arrangement type I; 5) cervical and second vertebrae free; 6) cranial bones not dermostosed; 8) sacral diapophyses dilated; 14) maxillary arch complete; 20) frontoparietals not fused to proötics; 21) temporal arcade lacking; 30) sphenethmoid usually divided; 35) mandible lacking odontoids; 37) alary processes of hyoid plate broad and wing-like; 38) cricoid cartilage divided ventrally; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on the body of the hyoid plate, near the midline; 45) first finger shorter than second; 47) amplexus inguinal in known species. All Myobatrachinae exhibit free intervertebral discs and non-imbricate neural arches. The transverse processes of all vertebrae are shortened in some genera. *Metacrinia* sometimes has prezygapophyses on the anterior end of the coccyx. The presence of free intervertebral discs and small prevomerine bones are the most diagnostic osteological characteristics of the subfamily. Within the subfamily, there is an evolutionary trend toward the reduction of bone in the skull; this reduction

is reflected in the frontoparietal fontanelle, size of the nasal bones, massiveness of the maxillary arch, divided sphenethmoid, and reduction in the size of the bones of the anterior palate.

Two groups of myobatrachine genera tend to be segregated on the bases of several characters. *Uperoleia* is the only genus with vertical pupils, and the only one lacking a frontoparietal fontanelle. *Glauertia* and *Uperoleia* have two large, compressed, metatarsal tubercles—in the other myobatrachine genera, both metatarsal tubercles are small and not compressed, or the outer absent (*Crinia: darlingtoni, haswelli, laevis,leai, rosea,* and *victoriana;* and *Taudactylus acutirostris).* The quadratojugal bones are deep (Figs. 65, 69, and 71) in *Crinia, Glauertia,* and *Uperoleia,* but more slender in the other genera. The nasal bones are comparatively large in *Glauertia, Metacrinia, Myobatrachus,* and *Uperoleia.* In these genera, the occipital condyles are larger than those of *Crinia, Pseudophryne,* and *Taudactylus.* The zygomatic rami of the squamosals are relatively short in *Glauertia, Metacrinia, Myobatrachus,* and *Uperoleia;* in *Crinia, Pseudophryne,* and *Taudactylus* the zygomatic rami are longer. Loss of the teeth of the maxillary arch is characteristic of all genera of the subfamily, except *Crinia* and *Taudactylus. Uperoleia rugosa* (two species are included under this name, see Littlejohn, 1968) and *U. mjoebergi* have teeth on the maxillary arch, but *U. marmorata* lacks maxillary teeth. All myobatrachines except some species of *Crinia* lack prevomerine teeth. *Crinia* and *Pseudophryne* differ from the other myobatrachines in having no *pars scapularis (m. depressor mandibulae);* all other myobatrachines have two slips in the *m. depressor mandibulae.*

Myobatrachine tadpoles have labial papillae only lateral to the tooth rows and beak—unlike other leptodactylids, the myobatrachines have an anterior and a posterior interruption of the labial papillae. The tooth rows are 1/3 to 2/3 in the known taxa. About one-half of the species of *Crinia* (*laevis* complex) and *Glauertia* and *Uperoleia* lay their eggs in water and have normal tadpole development. In these species the eggs are small (Martin, 1968). In the *Crinia signifera* complex, *Metacrinia, Myobatrachus,* and *Pseudophryne* the eggs are large and laid on land, part or all of the larval development occurring in the absence of water (Martin, 1968). Data are unavailable for *Taudactylus,* which probably also lays its eggs on land. At least some of the "terrestrial breeders" of the genera *Crinia* and *Pseudophryne* hatch as tadpoles when the nest is inundated and rapidly begin feeding and behaving like normally aquatic tadpoles. Some *Crinia* and probably *Metacrinia nichollsi* and *Myobatrachus gouldii* have completely terrestrial development (Martin, 1968).

Noble (1930) named a new genus, *Indobatrachus,* for *Rana pusillus* Owen, a Lower Eocene frog from the Intertrappean beds of Bombay in peninsular India. He considered the fossil closest to *Crinia* and therefore placed it in the group now designated as Myobatrachinae. Noble argued that the presence of a toothless bufonid in the early Cenozoic of the northern land masses indicated a northern origin for the group. Parker (1940) and Hecht (1963) suggested that the remains of *Indobatrachus* were overinterpreted, but failed to say why or how they reached that conclusion. Noble's data are not incompatible with the osteological data I have for the Recent Myobatrachinae. However, *Indobatrachus* could also be interpreted as not being very distant from *Nesomantis* and *Sooglossus,* which may prove to be myobatrachines as well; these subjects are discussed more fully in the generic account of *Indobatrachus.*

Crinia Tschudi, 1838
(Fig. 65)

Crinia Tschudi, 1838, Mem. Soc. Sci. Nat. Neuchatel, 2:38 [Type-species by monotypy, *Crinia georgiana* Tschudi, 1838].

Ranidella Girard, 1853, Proc. Acad. Nat. Sci. Philadelphia, 6:421 [Type-species by monotypy, *Crinia (Ranidella) signifera* Girard, 1853].

Pternophrynus Lütken, 1863, Vid. Meddel. Foren., 1862:302 [Type-species by monotypy, *Pternophrynus verrucosus* Lütken, 1863].

Camariolius Peters, 1863, Mtber. k. Preuss. Akad. Wiss., Berlin, 1863:236 [Type-species by monotypy, *Camariolius varius* Peters, 1863].

Pternophryne Günther, 1867, Ann. Mag. Natur. Hist., (3)20:53 [Replacement name for *Pternophrynus* Lütken, 1863 (preoccupied by *Pternophrynus* Gill, 1863—Osteichthys) and hence taking the same type-species].

Diagnostic definition.—7) omosternum present, small and elongate; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed posterodorsally, narrow at base; 11) palatal shelf of premaxilla broad, moderately deeply incised; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla broadest anteriorly, narrowing posteriorly, small pterygoid process; 14) quadratojugal deep; 15) nasals small, short, narrowly separated medially; 16) nasals not in contact with maxillae or pterygoids; 17) nasals widely separated from frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae short and stocky; carotid artery passes above skull bones; 24) zygomatic ramus of squamosal short, knob-like; 25) otic ramus of squamosal long, not developed into an otic plate; 26) squamosal-maxillary angle about 65° if measured along main axis of maxilla; 27) columella present; 28) prevomers widely separated medially, fragmented, dentigerous processes present or not, bearing teeth or not; 29) palatines narrow, sliver-like, not reaching maxillae; 30) sphenethmoid small, divided; 31) anterior ramus of parasphenoid narrow, not keeled; 32) parasphenoid alae oriented at right angles to

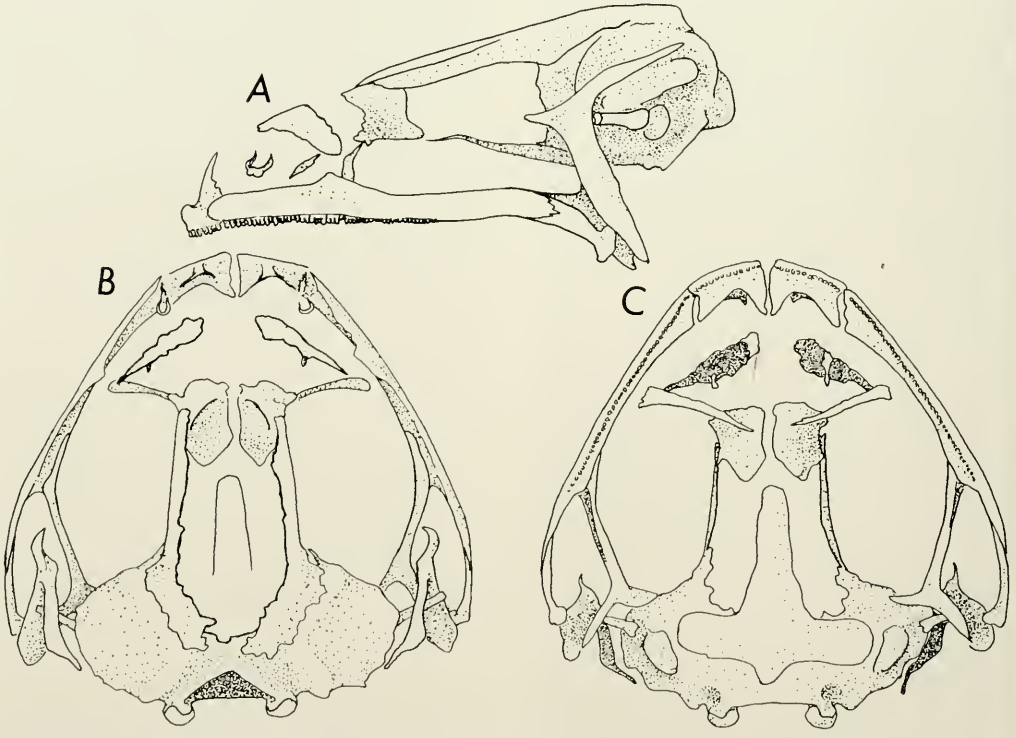

FIGURE 65. Lateral, dorsal, and ventral views of skulls of *Crinia signifera*. (A) KU 56243, × 8; (B-C) KU 56364, × 5.

anterior ramus, shortened and widely separated from median rami of pterygoids; 33) pterygoids small, anterior rami in short contact with maxillae; 34) occipital condyles small, stalked, widely separated medially; 36) terminal phalanges knobbed; 40) *m. depressor mandibulae* in one slip, *pars tympanicus;* 41) pupil horizontal; 42) males with median, subgular vocal sac; nuptial asperities on thumb; 43) body lacking glands; 44) tongue narrow, posterior edge free; 45) toes lacking webbing, but with prominent lateral fringes in *haswelli, tasmaniensis,* and the *signifera* complex; outer metatarsal tubercle present in all species except *darlingtoni, haswelli, laevis, leai, rosea,* and *victoriana;* digital tips narrow; 46) development direct in some species, "normal" in others; many species lay terrestrial eggs and have intraoval tadpoles, if the nest is inundated, the tadpole emerges and continues development as a free swimming tadpole; tadpoles have dextral vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly, narrowly interrupted posteriorly; 47) amplexus inguinal; 48) eggs small and numerous, laid in water, or eggs small and numerous and laid in terrestrial situations, or eggs large and few in number and laid in terrestrial situations; 49) adults small, males 14.5-30.0, females 19.0-32.5 mm. SVL; 50) tympanum concealed or visible externally.

Composition.—Parker (1940) recognized 13 kinds of *Crinia* one of which, *acutirostris,* is now placed in another genus. Moore (1961) recognized 16 species including *acutirostris.* Parker (1940), Main (1957), Moore (1961), and Martin (1968) recognized two species groups of *Crinia,* but included *acutirostris* in one of these groups. The *laevis* group contains six species—*darlingtoni, laevis, leai, lutea, rosea,* and *victoriana.* The *signifera* group includes eleven species—*georgiana, glauerti, haswelli, insignifera, parinsignifera, pseudinsignifera, riparia, signifera, sloanei, tasmaniensis,* and *tinnula.* As Moore (1961) pointed out, only a small part of *Crinia signifera* (*sensu* Parker) has been studied for sibling species, and the number of species in this complex and the genus should be expected to increase significantly in the next decade.

Distribution.—Australia (except for most of the western Eyrean subregion), eastern New Guinea, and Tasmania. Three species occur on Tasmania, one of which is endemic *(tasmaniensis),* and another very wide-spread and the only species to reach Papua (*signifera, sensu* Parker).

Remarks.—Perhaps the most interesting facet of the genus *Crinia* is the presence of several morphologically very similar species (*signifera* complex) with different calls, breeding biology, and/or tadpoles. *In vitro* crosses of these species led to the discovery that they were biospecies in the sense of Mayr (1963).

I have been able to study only one species osteologically; when additional studies are made on the skeletons of other species of *Crinia,* my diagnosis may be shown to be incomplete or in error. Considerable variation is evident in foot morphology and the expression of prevomerine teeth. Parker (1940) divided the genus into two groups on the basis of the division (dentigerous ramus separated from the part of the bone surrounding the choanae) of the prevomerine bones. The prevomerine bones are small but complete in most of the species of the *laevis* group, and divided in most species of the *signifera* group except *haswelli.* Parker (1940) suggested that *haswelli* might be the most primitive species of the genus on the basis of the pectoral girdle; the prevomerine anatomy of *haswelli* is not contrary to this suggestion. The two species groups of *Crinia* are separated on the basis of whether the skin of the venter is smooth (*laevis* group) or granular (*signifera* group). The species of the *laevis* group lack outer metatarsal tubercles and toe fringes, whereas the species of the *sig-*

nifera group have both outer metatarsal tubercles and lateral fringes on the toes (except *georgiana* and *glauerti*, which lack toe fringes, and *haswelli*, which lacks an outer metatarsal tubercle). Although the use of the presence or absence of prevomerine teeth as a major taxonomic character has been challenged by Main (1957), the character is useful as a secondary character in *Crinia*. Well developed prevomerine dentigerous processes and teeth occur in *leai*, *lutea*, *rosea*, and usually in *laevis* and *victoriana*, all of which are members of the *laevis* group. The only member of the *laevis* group which usually lacks prevomerine teeth is *darlingtoni*. Three species of the *signifera* group usually have well developed prevomerine dentigerous processes and teeth *(georgiana, glauerti,* and *haswelli);* the other species of the group almost invariably lack prevomerine teeth and prevomerine dentigerous processes.

Martin (1968) pointed out the variability in breeding habits in *Crinia*. Two species *(lutea* and *rosea)* have terrestrial development with the tadpole living in the jelly mass until metamorphosis. In several other species *(laevis* group and *riparia)* the eggs are laid out of water and the tadpole usually enters water sometime after completing early development. In most species of the *signifera* group and some of the *laevis* group, the eggs are laid in water (in small clumps) and the developmental pattern is that typified by *Rana*. Martin (1968) suggested that the different patterns of oviposition have little taxonomic significance in ascertaining species-group relationships.

Pseudophyryne Fitzinger, 1843
(Fig. 66)

Pseudophryne Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, *Phryniscus australis (partim)* Duméril and Bibron, 1841 (=*Pseudophryne semimarmorata* Lucas, 1892); see Parker (1940: 94) for a comment on this type-species designation].

Bufonella Girard, 1853, Proc. Acad. Nat. Sci. Philadelphia, 6:424 [Type-species by monotypy, *Bufonella crucigera* Girard, 1853].

Diagnostic definition.—7) omosternum present, small and narrow; 9) maxillary arch edentate; 10) alary processes of premaxillae directed dorsally, broad at base; 11) palatal shelf of premaxilla relatively narrow, palatal process elongate; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla of moderate width, pterygoid process small; 14) quadratojugal shallow; 15) nasals small, narrow, with slight median separation; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietals fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae stocky, broad; carotid artery passes above skull bones; 24) zygomatic ramus of squamosal very short, knob-like; 25) otic ramus of squamosal elongate, not expanded into otic plate; 26) squamosal-maxillary angle about 50°; 27) columella absent; 28) prevomers absent; 29) palatines reduced to splinter-like bones, not in contact with maxillae, widely separated medially; 30) sphenethmoid divided; 31) anterior ramus of parasphenoid broad posteriorly, narrowing towards palatines; 32) parasphenoid alae short, deflected posteriorly, not in contact with median rami of pterygoids; 33) pterygoids small, median and posterior rami short, anterior rami in short contact with maxillae, not reaching palatines; 34) occipital condyles large, stalked, widely separated medially; 36) terminal phalanges knobbed; 40) *m. depressor mandibulae* in one slip—*pars tympanicus*; 41) pupil horizontal; 42) males with median, subgular vocal sac; males lacking nuptial asperities; 43) parotoid, flank, and sometimes femoral glands present; 44) tongue long, narrow, posterior edge free; 45) toes free of webbing and lateral fringes, outer metatarsal tubercle present; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae

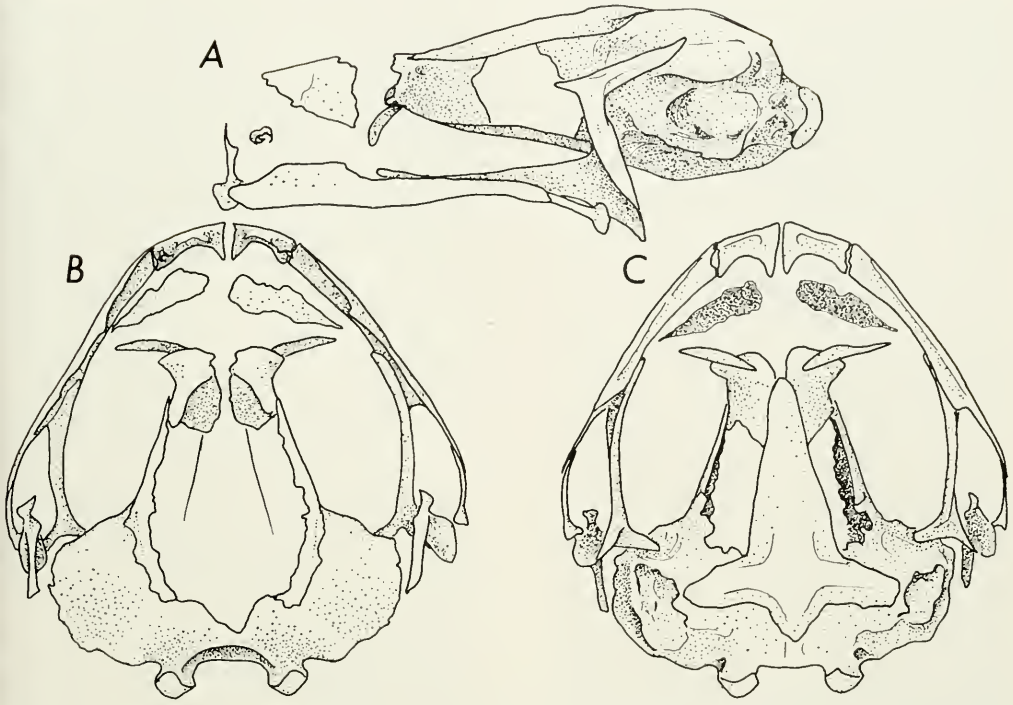

FIGURE 66. (A) Lateral, (B) dorsal, and (C) ventral views of a skull of *Pseudophryne bibroni* (KU 93588). (A, × 8; B-C, × 5).

broadly interrupted anteriorly, narrowly interrupted posteriorly, development occurs in either water or in jelly mass in terrestrial situations; 47) amplexus inguinal; 48) eggs laid singly in permanent water or in soil or moist sphagnum moss, number per clutch varies from 12 to over 100; 49) adults small, males 20-28, females 20-34 mm. SVL; 50) tympanum absent.

Composition.—Ten species are presently recognized: *australis, bibroni, coriacea, corroboree, dendyi, douglasi, guentheri, major, occidentalis,* and *semimarmorata.* Parker's (1940) study is the most recent review, although Moore's (1961) study of the frogs of eastern New South Wales treats several of the species of the genus.

Distribution.—Northwestern and southwestern Australia; and east of the Dividing Range from east-central Queensland to the Capital Territory; Tasmania.

Remarks.—*Pseudophryne* and *Crinia* are closely related and differ primarily in maxillary dentition, loss of the middle ear, and coloration and body glands. The two genera were placed in different families by taxonomists before Noble, because *Pseudophryne* lacks teeth and *Crinia* has teeth on the maxillary arch. *Metacrinia* is superficially similar to *Pseudophryne,* but differs markedly in the skull architecture and temporal musculature.

Taudactylus Straughan and Lee, 1966
(Fig. 67)

Taudactylus Straughan and Lee, 1966, Proc. Royal Soc. Queensland, 76:63 [Type-species by original designation, *Taudactylus diurnus* Straughan and Lee, 1966].

Diagnostic definition.—7) omosternum absent; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed very slightly posterodorsally, narrow at base; 11) palatal shelf of premaxilla relatively broad laterally, narrow medially, bearing

greatly elongated palatal process; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla of moderate width, narrowing posteriorly, pterygoid process minute; 14) quadratojugal shallow, long and thin; 15) nasals very small, widely separated medially; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle present, small and narrow; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae short, stocky; carotid artery passing dorsal to skull bones; 24) zygomatic ramus of squamosal short, thin, about one-third length of otic ramus, therefore proportionately longer than zygomatic rami of other myobatrachines; 25) otic ramus of squamosal long, not expanded medially into otic plate; 26) squamosal-maxillary angle about 55°; 27) columella present; 28) prevomers minute, fragmented, dentigerous rami absent, restricted to medial edges of choanae; 29) palatines narrow, widely separated medially; 30) sphenethmoid divided; 31) anterior ramus of parasphenoid long, narrow, reaching level of palatines, not keeled; 32) parasphenoid alae short, deflected posteriorly, not overlapped by median rami of pterygoids; 33) pterygoids comparatively large, anterior rami in short contact with maxillae, not reaching palatines; 34) occipital condyles small, stalked, widely separated medially; 36) terminal phalanges T-shaped; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median, subgular vocal sac; diffuse nuptial pad on thumb; 43) body lacking glands; 44) tongue long, narrow, posterior edge free; 45) toes not webbed, bearing distinct lateral fringes, outer metatarsal tubercle absent; 46-48); 49) males 24-27, females 27-31 mm. SVL; 50) tympanum concealed.

Composition.—Monotypic, *Taudactylus acutirostris* (Andersson).

Distribution.—Known only from four

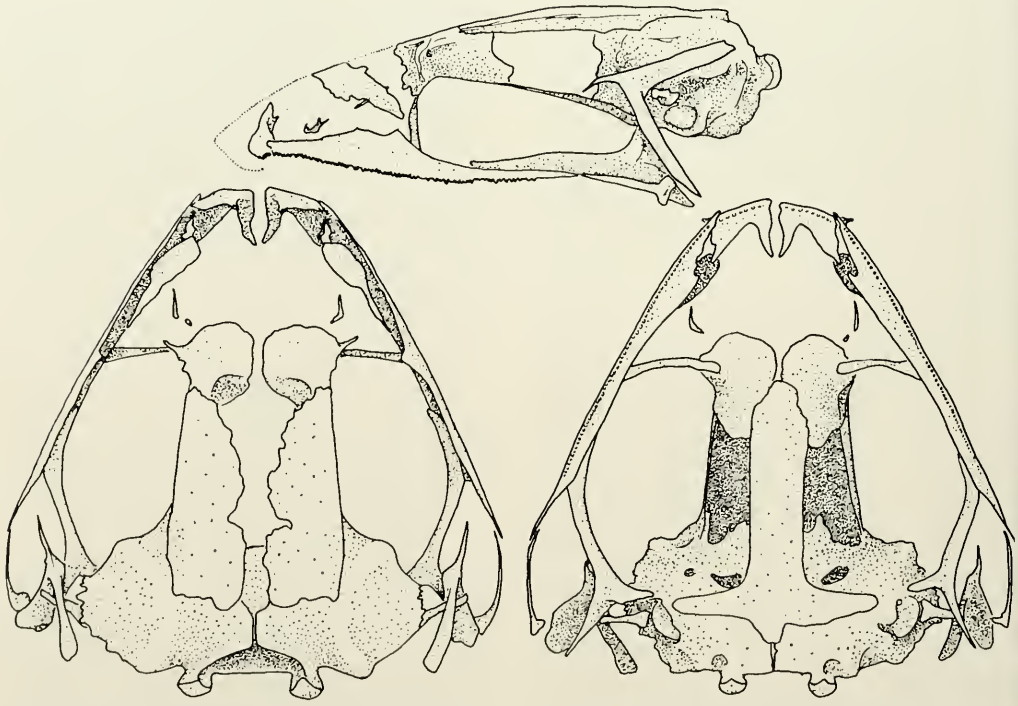

FIGURE 67. Lateral, dorsal, and ventral views of the skull of *Taudactylus acutirostris* (KU 124233, × 5).

localities in the Great Dividing Range in Queensland.

Remarks.—Parker (1940) included *acutirostris* in the *Crinia signifera* group. He was familiar with the osteology of the anterior palate, but did not notice the T-shaped terminal phalanges and the widely separated nasal bones. In external appearance, *Taudactylus* is not especially distinctive. The pad-like digital tips and the pointed snout (which overhangs the jaw) are the only distinctive external features of the monotypic genus. The type-species *(diurnus)* is not distinguishable from *Crinia acutirostris*, and therefore *acutirostris* is placed in the genus *Taudactylus* (Straughan and Main, 1966).

Taudactylus acutirostris has lateral fringes on the toes and lacks an outer metatarsal tubercle like *Crinia haswelli*; *C. haswelli* differs from *Taudactylus* in having narrow digital tips knobbed terminal phalanges), a rounded snout, and prevomerine teeth. Although I consider *Crinia* and *Taudactylus* related, I do not believe that any of the currently known species of *Crinia* (see page 93) will prove to be *Taudactylus*. *Taudactylus* most closely resembles *Crinia* and *Pseudophryne* osteologically but is obviously different in its lack of a large frontoparietal fontanelle.

Glauertia Loveridge, 1933
(Fig. 68)

Glauertia Loveridge, 1933, Occ. Papers Boston Soc. Nat. Hist., 8:89 [Type-species by original designation, *Glauertia russelli* Loveridge, 1933].

Diagnostic definition.—7) omosternum present, small; 9) maxillary arch edentate; 10) alary processes of premaxillae directed very slightly anterodorsally; 11) palatal shelf of premaxillae of moderate width with elongate palatal process; 12) facial lobe of maxilla relatively shallow; 13) palatal shelf of maxilla of moderate width, pterygoid process small; 14) quadratojugal very deep; 15)

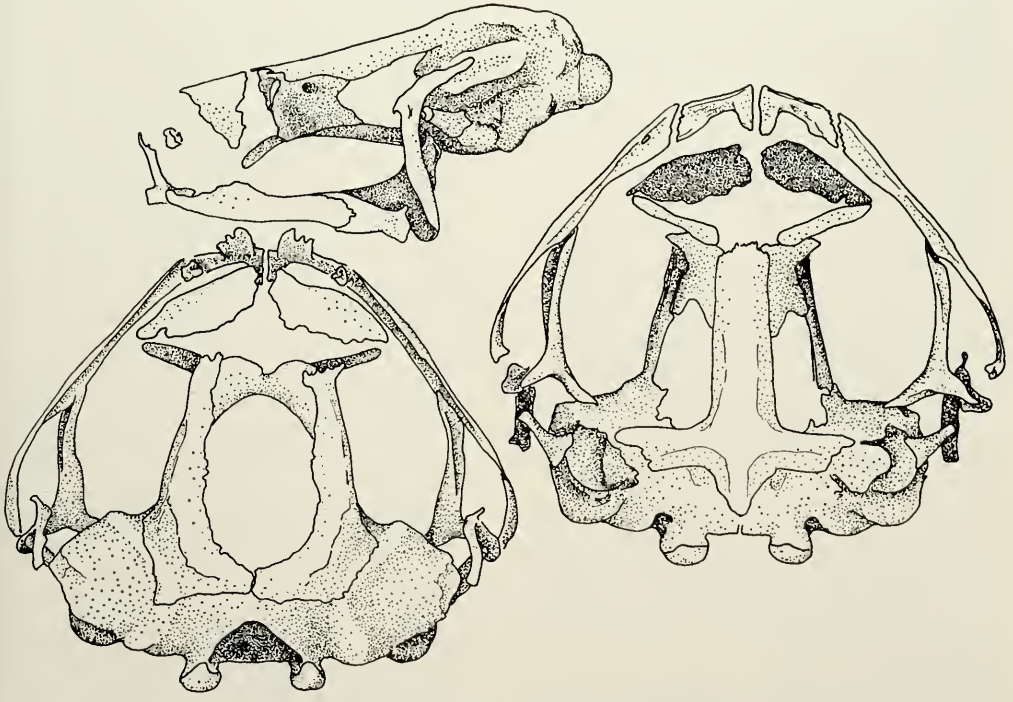

FIGURE 68. Lateral, dorsal, and ventral views of a skull of *Glauertia russelli* (Western Australia Museum R22920, × 5).

nasals moderate sized, narrowly separated medially; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences poorly developed; 23) cristae paroticae short, stocky; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal minute; 25) otic ramus of squamosal relatively long, no otic plate; 26) squamosal-maxillary angle about 70°; 27) columella present; 28) prevomers absent; 29) palatines broad, not in contact with maxillae, widely separated medially; 30) sphenethmoid entire, not extending anteriorly to nasals; 31) anterior ramus of parasphenoid broad, lacking median keel; 32) parasphenoid alae oriented at right angles to anterior ramus, short and broad, widely separated from median rami of pterygoids; 33) pterygoids relatively small, anterior rami in short contact with maxillae; 34) occipital condyles moderately large, stalked, widely separated medially; 36) terminal phalanges knobbed; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median, subgular vocal sac; lacking nuptial asperities on thumb; 43) body lacking glands or with only very diffuse flank glands; 44) tongue narrow, free posteriorly; 45) toes one-fourth to one-half webbed, outer metatarsal tubercle present and as large as, and compressed like, inner metatarsal tubercle, digital tips narrow; 46) larvae aquatic, not described; 47) amplexus inguinal; 48) eggs numerous, small, laid in ponds; 49) adults 22-32 mm. SVL; 50) tympanum concealed.

Composition.—Parker (1940) recognized three species—*mjoebergi, orientalis,* and *russelli.* I consider *mjoebergi* a species of *Uperoleia,* and tentatively recognize *orientalis* and *russelli* as specifically distinct members of *Glauertia.*

Distribution.—The two norminal species of *Glauertia* are known from a half-dozen localities in the northern territories of Australia.

Remarks.—Parker (1940) named *Glauertia orientalis* as the second species of the genus, and placed *Pseudophryne mjoebergi* Andersson in *Glauertia* as well. Harrison (1927) suggested that *mjoebergi* might be a synonym of *Uperoleia marmorata,* but Parker (1940) dismissed the suggestion with the remark ". . . *Pseudophryne mjöbergi* . . . appears to be referable to the genus *Glauertia.*" Parker did not offer evidence for or against this statement. Parker's (1940) diagnosis of *Glauertia* is clearly based only on *orientalis* and *russelli.* Loveridge (1933) considered *Glauertia* related to *Pseudophryne* and *Uperoleia,* and later (1935) stated that *Glauertia* was most closely related to *Pseudophryne.* Parker (1940) did not comment on the relationships of *Glauertia* other than "The species of this genus appear . . . to be descended from some Criniine stock." He apparently considered *Glauertia* merely webbed *Crinia. Glauertia* resembles *Crinia* only in the very large frontoparietal fontanelle; however, the large frontoparietal fontanelle is characteristic of not only *Crinia* and *Glauertia,* but also of *Metacrinia, Myobatrachus,* and *Pseudophryne.* In external characters, *Glauertia* is most like *Uperoleia*; the two genera differ in pupil shape, body glands, degree of digital webbing, and in the size of the frontoparietal and nasal bones. The similarity in foot morphology and in the squamosal architecture of *Glauertia* and *Uperoleia* strongly suggest that they are closely related. The digits are fringed in *Uperoleia* and webbed (less than one-half) in *Glauertia*—this difference is one of degree. *Uperoleia* has well defined parotoid and flank glands whereas *Glauertia* has diffuse glands along the flank. The metatarsal tubercles in both genera are enlarged and compressed; in no other myobatrachine frogs is there comparable development of the metatarsal tubercles.

Pseudophryne mjoebergi is more sim-

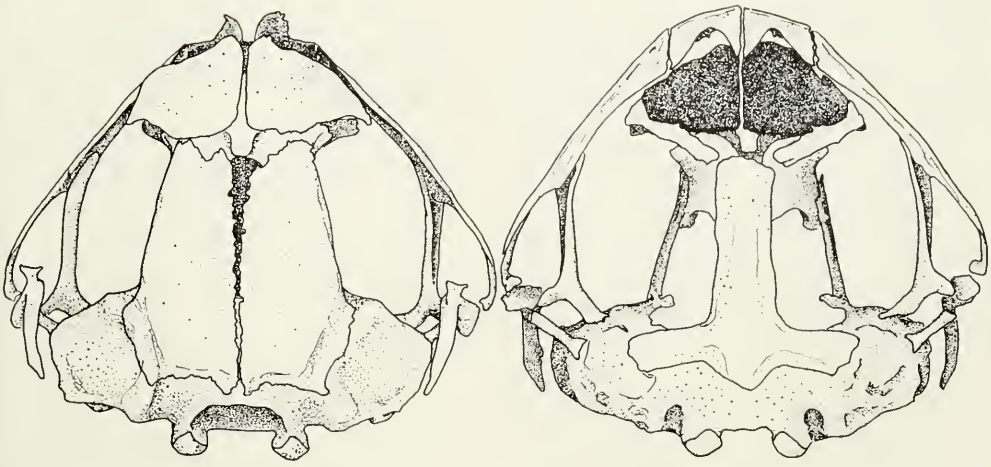

FIGURE 69. Dorsal and ventral views of skull of *Uperoleia rugosa* (KU 109861, × 5).

ilar to *Uperoleia rugosa* than to *Glauertia russelli* and is therefore placed in *Uperoleia*. Until the pupil shape (in life) and cranial osteology of *mjoebergi* are known, this action should be regarded as tentative. The relationships of the species of these two genera are seriously in need of study; the six species included in the two genera seem more closely interrelated than is indicated by the generic classification.

Uperoleia Gray, 1841
(Figs. 69-70)

Uperoleia Gray, 1841, Ann. Mag. Natur. Hist., (1)7:90 [Type-species by monotypy, *Uperoleia marmorata* Gray, 1841].

Hyperolia Cope, 1865, Rev. Natur. Hist., 5:108 [Emendation of *Uperoleia* Gray, 1841, hence taking same type-species. As pointed out by Parker (1940), it is best to retain Gray's spelling].

Diagnostic definition.—7) omosternum small; 9) maxillary arch toothed or not, if toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed dorsolaterally, wide at base; 11) palatal shelf of premaxilla of moderate width, palatal process elongate; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla of moderate width, pterygoid process small; 14) quadratojugal very deep; 15) nasals large, in broad median contact; 16) nasals not in contact with maxillae or pterygoids; 17) nasals in tenuous contact with frontoparietals; 18) frontoparietal fontanelle absent; 19) frontoparietals not ornamented or only slightly roughened posteriorly; 22) epiotic eminences obsolete; 23) cristae paroticae short, stocky; carotid artery lies on skull in shallow groove median to epiotic eminences; 24) zygomatic ramus of squamosal minute; 25) otic ramus of squamosal long, no otic plate; 26) squamosal-maxillary angle about 50°; 27) columella present; 28) prevomers reduced to minute fragments lying on inner edge of choanae; 29) palatines broad, widely separated medially, not in contact with maxillae; 30) sphenethmoid usually entire, extending an-

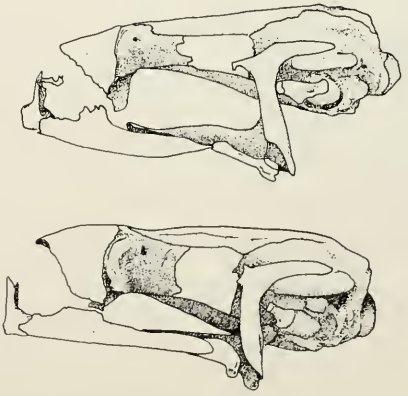

FIGURE 70. Lateral views of the skulls of (top) *Metacrinia nichollsi* (KU 110332, × 4.8) and (bottom) *Uperoleia rugosa* (KU 109861, × 3.2).

teriorly beneath posterior edge of nasals; 31) anterior ramus of parasphenoid broad, not keeled; 32) parasphenoid alae short, deflected posteriorly, not overlapped by median rami of pterygoids; 33) pterygoids relatively massive, anterior rami in short contact with maxillae; 34) occipital condyles relatively small, not stalked, widely separated medially; 36) terminal phalanges knobbed; 40) *m. depressor mandibulae* in two slips; 41) pupil vertical in life, rhomboidal in preserved specimens; 42) male with median, subgular vocal sac; thumb of male swollen in breeding season, lacking nuptial asperities; 43) large parotoid and flank glands present; 44) tongue large, round, posterior one-third free; 45) toes fringed, not webbed, outer metatarsal tubercle present, metatarsal tubercles enlarged, compressed, digital tips narrow; 46) larvae with dextral vent, 1/3 tooth rows, labial papillae broadly interrupted anteriorly, narrowly interrupted posteriorly; 47) amplexus inguinal; 48) eggs small, laid singly in ponds, marshes; over 200 eggs per clutch; 49) males 20-29, females 21-33 mm. SVL; 50) tympanum concealed; 51) anal flap fimbriated, at least in females.

Composition.—Loveridge (1935) and Moore (1961) considered *Uperoleia* to be monotypic. Parker (1940) recognized two species, the toothed *marmorata* and the toothless *rugosa*. Littlejohn (1968) recognized two sibling species under the specific name *Uperoleia rugosa*. I consider *Glauertia mjoebergi* to be a *Uperoleia*. Therefore, the genus *Uperoleia* contains four recognized species—*marmorata, mjoebergi,* and two kinds of *rugosa*.

Distribution.—Littlejohn (1968) characterized both species of *rugosa* as being part of the "wide-ranging component." Knowledge of the distribution of *Uperoleia* is spotty, but the genus seems to range through all coastal areas of the continent. It does not occur on New Guinea or Tasmania.

Remarks.—The inclusion of *mjoebergi* in the genus *Uperoleia* does not require an expansion of the generic definition.

Metacrinia Parker, 1940
(Figs. 70-71)

Metracrinia Parker, 1940, Novitates Zool., 42: 93.

Metacrinia Parker, 1940, Novitates Zool., 42: 93 [Type-species by original designation, *Pseudophryne nichollsi* Harrison, 1927].

Diagnostic definition.—7) omosternum small; 9) maxillary arch edentate; 10) alary processes of premaxillae directed dorsally, wide at base; 11) palatal shelf of premaxilla narrow, palatal process elongate; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla narrow, no pterygoid process; 14) quadratojugal of moderate depth; 15) nasals relatively small, in median contact; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae broad, stocky; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal short, bulbous; 25) otic ramus of squamosal long, no otic plate; 26) squamosal-maxillary angle about 65°; 27) columella present; 28) prevomers minute, fragmented, dentigerous rami lost, widely separated medially; 29) palatines narrow, not in contact with maxillae, widely separated medially; 30) sphenethmoid entire, extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid broad, not keeled, extending anteriorly to between palatines; 32) parasphenoid alae short, deflected posteriorly, not overlapped laterally by median rami of pterygoids; 33) pterygoids small, median rami short, anterior rami long but not reaching palatines; 34) occipital condyles large, not stalked, widely separated medially; 36) terminal phalanges knobbed; 40) *m. de-*

FIGURE 71. Dorsal and ventral views of the skull of *Metacrinia nichollsi* (KU 110332, × 7).

pressor mandibulae in two slips; 41) pupil horizontal; 42) males with median, subgular vocal sac; lacking nuptial asperities; 43) body lacking glands; 44) tongue narrow, free posteriorly; 45) toes lacking webbing or lateral fringes, outer metatarsal tubercle present, digital tips narrow; 46) development direct; 47-48); 49) adults less than 25 mm. SVL; 50) tympanum concealed.

Composition.—The type-species is the only known species.

Distribution.—Western Australia, west of the Darling Range and south of Geographe Bay (Parker, 1940).

Remarks.—*Metacrinia nichollsi* looks like a drab species of *Pseudophryne*. Parker (1940) named the genus when he discovered that *nichollsi* has a middle ear. The genus differs from *Pseudophryne* in the nature of the *m. depressor mandibulae*, size of the nasal bones, and the size of the zygomatic ramus of the squamosal. The large occipital condyles of *Metacrinia* suggest a relationship to the *Glauertia-Uperoleia* complex or to *Myobatrachus*. *Metacrinia* apparently has completely terrestrial development (Parker, 1940, Martin, 1968), but observations on the life history of the species are entirely lacking.

Myobatrachus Schlegel, 1850
(Fig. 72)

Myobatrachus Schlegel, 1850, Proc. Zool. Soc. London, p. 9 [Type-species by monotypy, *Myobatrachus paradoxus* Schlegel, 1850].

Myiobatrachus Schlegel, 1858, Handlied. Dierk., 2:59 [Emendation of *Myobatrachus* Schlegel, 1850].

Chelydobatrachus Günther, 1859, Cat. Batr. Sal. British Mus., p. 63 [Type-species by monotypy, *Breviceps gouldii* Gray, 1841].

Diagnostic definition.—7) omosternum absent; 9) maxillary arch edentate; 10) alary processes of premaxillae minute, knob-like; 11) palatal shelf of premaxilla narrow, palatal process elongate; 12) facial lobe of maxilla minute; 13) palatal shelf of maxilla narrow, pterygoid process large; 14) quadratojugal in tenuous contact with maxilla, relatively shallow; 15) nasals large, in median contact; 16) nasals narrowly separated from maxillae, broadly separated from pterygoids; 17) nasals in tenuous contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae short, stocky; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal absent; 25) otic ramus of squamosal large, but not forming otic plate; 26) squamosal-maxillary angle not

measurable; 27) columella present; 28) prevomers absent; 29) palatines massive, bearing odontoid ridges, articulating with maxillae, widely separated medially; 30) sphenethmoid divided dorsally, complete ventrally; 31) anterior ramus of parasphenoid broad, short, not keeled; 32) parasphenoid alae short, oriented at right angles to anterior ramus, widely separated from median rami of pterygoids; 33) pterygoids small and heavy, median rami short, anterior rami in long contact with maxillae, reaching palatines; 34) occipital condyles large, not stalked, widely separated medially; 36) terminal phalanges knobbed; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median, subgular vocal sacs; nuptial asperities lacking; 43) body lacking glands; 44) tongue long, narrow, free posteriorly; 45) toes lacking webbing and lateral fringes, outer metatarsal tubercle present, digital tips narrow; 46) development apparently direct; 47-48); 49) adults to 60 mm. SVL; 50) tympanum concealed; 51) head disproportionately small compared to body, limbs short.

Composition.—Monotypic; Schlegel's *paradoxus* is a synonym of Gray's *gouldii*.

Distribution.—Western Australia.

Remarks.—Schlegel (1850) named the type-species of *Myobatrachus* with the specific epithet *paradoxus;* Parker (1940) characterized the body shape as "globose." On first impression, *Myobatrachus* is a bizarre frog. The head is incongruously small compared to the size and shape of the body. The great reduction in the size of the head is probably an adaptation to a myrmecophagous livelihood. The external adaptations are no less striking than the adaptations of the skull. The anterior portion of the skull is reduced in size whereas the posterior portion of the skull is not. The alary processes of the premaxillae are minute (Fig. 11) and the maxillae are very small anteriorly. The nasal bones form an arch over the nasal capsules. The reduction in the size and strength of the anterior skull bones is compensated

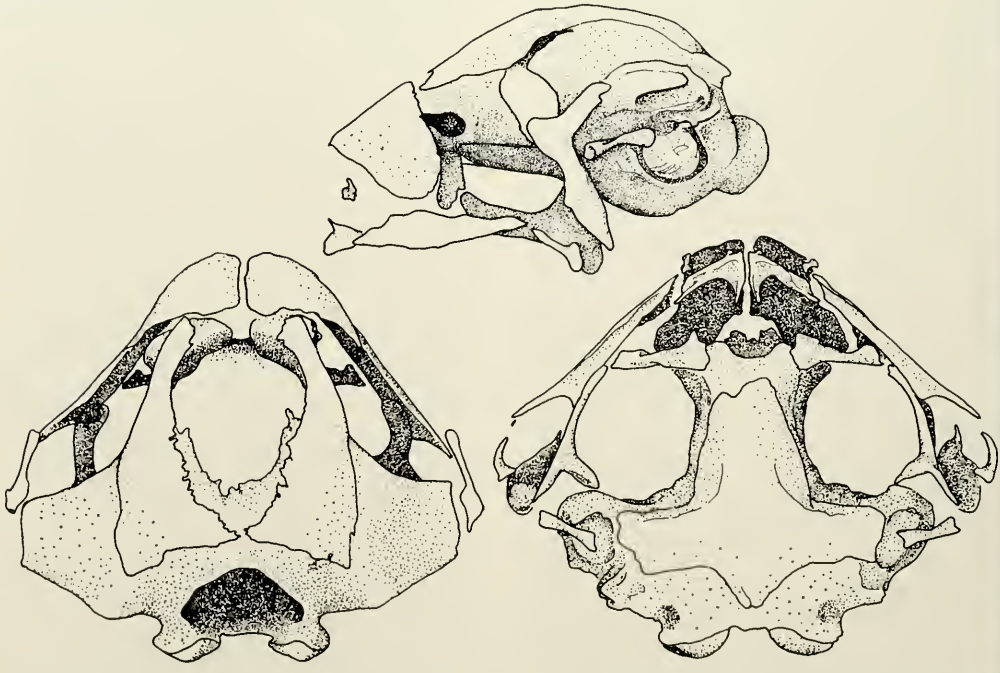

FIGURE 72. Lateral, dorsal, and ventral views of skull of *Myobatrachus gouldii* (KU 110333, × 7.5).

for by the enlargement of the palatines which serve as the major supportive element of the anterior portion of the skull. Judging from the size of the body and the size of the posterior portion of the skull, *Myobatrachus* was probably a large frog with a normal-sized head before it adapted to an ant-eating habit.

Myobatrachus seems less distantly removed from *Glauertia, Metacrinia,* and *Uperoleia,* than from the criniine genera. In spite of the reduction in the size of the anterior cranial bones, the skull of *Myobatrachus* is primitive in many respects. The occipital condyles are large and massive and the nasals are large and in median contact. The size of the nasals, however, could more accurately reflect a post-reduction strengthening of the skull.

†Indobatrachus Noble, 1930

Indobatrachus Noble, 1930, Amer. Mus. Novitates, 401:2 [Type-species by original designation, *Rana pusilla* Owen, 1847].

Parker (1940) and Hecht (1963) suggested that the fossils of *Indobatrachus pusillus* were "over-interpreted." Without actually saying so, they implied that its familial relationships are in doubt. The numerous figures in Noble's (1930) paper treat most of the character complexes used in family-level classification of frogs. The bicotylar coccyx, dilated sacral diapophyses, shortened transverse processes of the presacral vertebrae, and apparently free intervertebral discs all point to myobatrachine relationships for *Indobatrachus.* Noble (1930) argued that the strongly arched clavicles indicated that the pectoral girdle was arciferal; strongly arched clavicles are also found in some of the small African ranids (Arthroleptinae), which have firmisternal pectoral girdles in the strict sense. What details of the skull are preserved are not inconsistent with the cranial osteology of *Crinia, Nesomantis, Sooglossus,* or the arthroleptine ranids.

Before the systematic importance of *Indobatrachus* can be fully appreciated, more detailed study must be made of the osteology of the sooglossids and the arthroleptine ranids. The available evidence is adequate to associate the fossil with the Myobatrachinae. When our knowledge of the osteology of the Ranidae is improved, the fossil may prove significant in evaluating the primitiveness of some ranid subfamilies and clarify the supposed relationship between the Microhylidae and Ranidae.

Heleophryninae Noble, 1931

Heleophryninae Noble, 1931:498.
Heleophrynidae: Hoffman, 1935:2.

Heleophryne is the sole African representative of the Leptodactylidae. Most authors have accorded *Heleophryne* subfamilial recognition and a few have argued that it is a monotypic family. Noble (1931) associated it with the bufonoid frogs, and has been followed by most subsequent authors. Reig (1958) accorded *Heleophryne* familial rank in his "Superfamilia B" (=Ranoidea of Davis, 1935). The evidence used in associating *Heleophryne* with ranoid frogs is meager. Hoffman (1930) described what he believed to be the pectoral girdle of an adult *Heleophryne regis,* and contended that the pectoral girdle of this genus was arciferal in juveniles and subadults, but firmisternal in old adults. Du Toit (1930) described the internal and external cranial anatomy of *Heleophryne regis*; in external cranial anatomy the skull was ranid-like. Hoffman's old adult *Heleophryne* was a ranid of the genus *Hylambates,* as was the specimen du Toit used to describe the external cranial anatomy (du Toit, 1931). Latsky (1930) reported that the sacral vertebra of Heleophryne is diplasiocoelus and the thigh musculature is intermediate between the pelobatid and bufonid patterns. My investigation of the vertebral column in *Heleophryne* resulted in the conclusion that the vertebral centra exhibit a paedomorphic condition, in which the tissue of the intervertebral body is not divided by invad-

ing arcs of connective tissue. A similar situation was reported by Griffiths (1960) for *Nesomantis* and *Sooglossus*. Therefore, all the evidence thus far advanced in support of ranoid relationships of *Heleophryne* is erroneous.

Although *Heleophryne* has several pelobatid-like traits, it is clearly a member of the Bufonoidea. The genus is not clearly distinct from the primitive Australo-Papuan Cycloraninae in that it has a type II cervical cotylar arrangement, fused cervical and second vertebrae, and a vertical pupil, and lacks an outer metatarsal tubercle. The relationship of the prevomerine dentigerous processes and choanae of *Heleophryne* is unique among leptodactylid frogs, as is its torrent-adapted tadpole lacking horny beaks. Amplectic data are not available for *Heleophryne*; I anticipate that it will be found to engage in inguinal amplexus. The thigh musculature of *Heleophryne* is, in several respects, intermediate between that of pelobatids and bufonoids, suggesting an independent origin of the Heleophryninae from the Pelobatidae, though not demanding that this was the evolutionary course.

Because only a single genus is included in this subfamily, I have not separated subfamily characters from generic characters. All 50 characters are listed in the generic account (insofar as they are known).

Heleophryne Sclater, 1898
(Fig. 73)

Heleophryne Sclater, 1898, Ann. South African Mus., 1:110 [Type-species by monotypy, *Heleophryne purcelli* Sclater, 1898].

Diagnostic definition.—1) sternum cartilaginous; 2) vertebral shield lacking; 3) transverse processes of anterior presacral vertebrae not expanded; 4) cervical cotylar arrangement type II; 5) cervical and second vertebrae fused; 6) cranial bones not dermostosed; 7) omosternum present, moderately large; 8) sacral diapophyses round; 9) maxillary arch toothed, teeth blunt, pedicellate; 10) alary processes of premaxillae directed dorsolaterally, relatively broad at base; 11) palatal shelf of premaxilla nar-

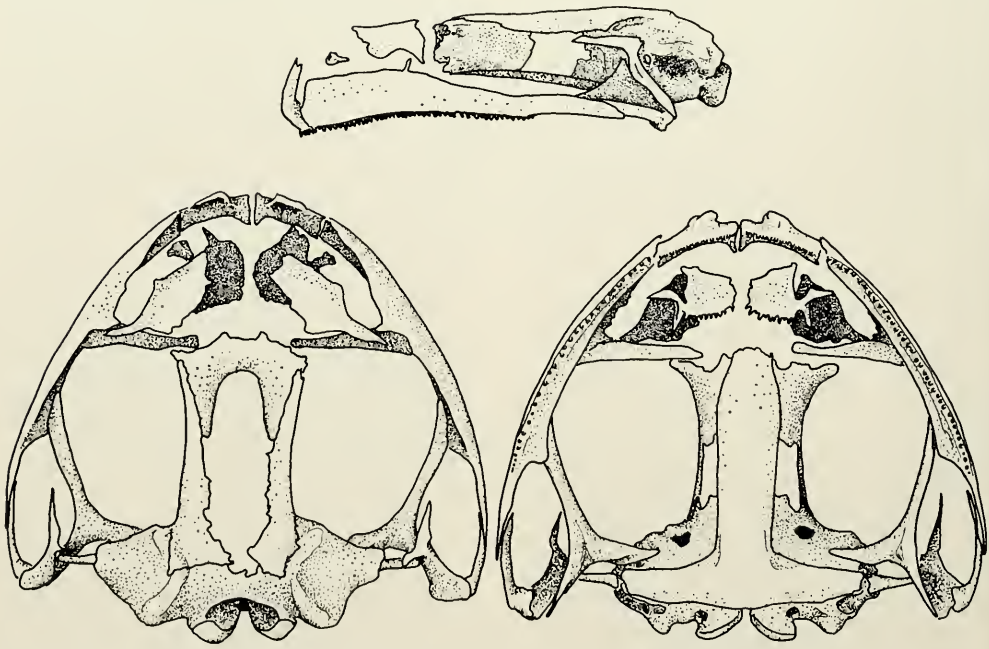

FIGURE 73. Lateral, dorsal, and ventral views of skull of *Heleophryne natalensis* (KU 105925, × 2.5).

row, palatal process large; 12) facial lobe of maxilla relatively shallow; 13) palatal shelf of maxilla of moderate width, pterygoid process large; 14) maxillary arch complete, quadratojugal present, shallow; 15) nasals small, widely separated medially; 16) nasals not contacting maxillae or pterygoids; 17) nasals widely separated from frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 20) frontoparietal not fused to proötic; 21) temporal arcade lacking; 22) epiotic eminences obsolete; 23) cristae paroticae long, slender; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal short, about as long as otic ramus; 25) otic ramus of squamosal short, no otic plate; 26) squamosal-maxillary angle about 50°; 27) columella present; 28) prevomers entire, large, toothed, dentigerous processes lie anterior to choanae; 29) palatines widely separated medially, narrow; 30) sphenethmoid entire, extending anteriorly beneath posteromedial corners of nasals or not reaching nasals; 31) anterior ramus of parasphenoid broad, not keeled, extending anteriorly to point between palatines; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively small, anterior rami in short contact with maxillae, widely separated from palatines; 34) occipital condyles moderately large, not stalked, narrowly separated medially; 35) mandible lacking odontoids; 36) terminal phalanges T-shaped; 37) alary processes on hyoid plate on narrow stalks; 38) cricoid cartilage not divided ventrally; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 40) *m. depressor mandibulae* in two slips; 41) pupil vertical; 42) males with median, subgular vocal sac; 43) body lacking glands; 44) tongue large, posterior edge free; 45) toes at least one-half webbed, outer metatarsal tubercle lacking, digital tips bearing large pads, first finger shorter than second; 46) larvae with median vent, 4/11–4/17 tooth rows, labial papillae not interrupted, beak absent; 47-48); 49) adults 35-65 mm. SVL; 50) tympanum visible externally.

Composition.—Poynton (1964) recognized three species—*natalensis, purcelli,* and *rosei.* At present, *purcelli* has three recognized subspecies.

Distribution.—South Africa from the Cape Peninsula to eastern Transvaal.

Remarks.—Excepting the considerable knowledge of the tadpoles, nothing is known about the life history of *Heleophryne.* Pre- and post-oviposition behavior and oviposition sites are useful systematic characters (at least in leptodactylid classification).

Ceratophryinae Tschudi, 1838

Ceratophrydes Tschudi, 1838:81.
Ceratophrydidae: Cope, 1863:50.
Ceratophryinae: Parker, 1935:511.
Ceratophryninae: Reig, 1960a:117.
Ceratophrynidae: Reig and Cei, 1963:181.
Ceratophryidae: Tihen, 1965:313.

The concept of a family group for *Ceratophrys* and its relatives has been advocated for more than 100 years. During this period the content and the rank of the group varied considerably. Most South American authors accord the group familial recognition, whereas most North American and European authors insist that the group is at best subfamilially distinct. The South American authors consider the Ceratophryidae to be more closely related to the Bufonidae than to the Leptodactylidae. Noble (1931) included the cerotaphryine genera in his Pseudinae (=Pseudidae, Ceratophryinae, and Telmatobiinae as used here). Parker (1935) pointed out that *Pseudis* was not related to the group but belonged to a monotypic subfamily of the Hylidae. He used the next oldest family group name for the remaining members of the group (Ceratophryinae) The content of the group was not significantly changed, inasmuch as it continued to embrace most of the Neotropical leptodactylid genera.

The following characters are diagnostic for the subfamily and consistent within the included genera: 1) sternum cartilaginous; 2) vertebral shield present, dermostosed; 3) transverse processes of anterior presacral vertebrae widely expanded; 4) cervical cotylar arrangement type III; 5) cervical and second vertebrae usually free, fused superficially in old specimens; 6) cranial bones dermostosed; 8) sacral diapophyses rounded; 9) maxillary arch toothed, teeth fang-like, non-pedicellate, few in number; 14) maxillary arch complete, maxillae and quadratojugals fused; 18) frontoparietal fontanelle lacking; 19) frontoparietals extensively ornamented with dermostoic pattern; 20) frontoparietals fused to proötics; 21) temporal arcade complete; 27) columella present; 34) occipital condyles large, closely juxtaposed or confluent; 36) terminal phalanges knobbed; 37) hyoid plate lacking alary processes, cornu very broad; 38) cricoid cartilage not divided ventrally; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 46) larvae with median vent, labial papillae not interrupted; 47) amplexus axillary; 48) eggs laid in gelatinous masses in water, eggs small and numerous.

Three Recent genera are usually included in this subfamily—*Ceratophrys, Chacophrys,* and *Lepidobatrachus.* The genus *Chacophrys* is not considered valid by me, because the diagnostic characteristics are all expressions of the paedomorphic skeleton of the type-species, *C. pierotti*; *Chacophrys* is here placed as a synonym of *Ceratophrys.*

Boulenger (1882, 1919) and Cochran (1955) included members of several genera in their *Ceratophrys.* Boulenger combined the species of *Ceratophrys, Lepidobatrachus, Odontophrynus,* and *Stombus* in his *Ceratophrys.* Neither author nomenclatorally recognized the Ceratophryinae, although Cochran (1955) used the term "broad-headed leptodactylids" in the sense of Miranda-Ribeiro's (1926) Ceratophrydidae. Boulenger and Cochran recognized two groups of *Ceratophrys*; one with a dorsal shield (*Ceratophrys* in the strict sense) and one lacking the shield (*Stombus auctorum).*

The genera of the "broad-headed leptodactylids" (the Ceratophryinae concept of Boulenger, Cochran, and Miranda-Ribeiro) were separated on the basis of the development of a fleshy "horn" on the upper eyelid and the degree of webbing of the toes. The genera included in this group by previous authors are placed in two subfamilies by me, the Ceratophryinae and Telmatobiinae. The genera belonging to the latter subfamily are placed in three tribes. The subfamilial and tribal separation of these genera is supported by osteological data. Cei (1965) and Cei, Erspamer, and Roseghini (1968) demonstrated that *Ceratophrys* and *Lepidobatrachus* differed from *Odontophrynus* and *Stombus auctorum* in skin proteins, and that the latter two genera were like leptodactylids insofar as skin proteins are concerned. Cei (1965) separated the Leptodactylidae, as here used, into two families, the Ceratophryidae and the Leptodactylidae, but Cei, Erspamer, and Roseghini (1968) included *Odontophrynus* in the Ceratophrydidae.

Limeses (1964, 1965) presented data that she regarded as suggestive of a closer alliance between bufonids and ceratophryids than between the latter and leptodactylids. She was unaware of the variability of the *m. depressor mandibulae* in the Leptodactylidae. Her data perhaps are useful in analyzing trends within subfamilies but they are not convincing enough to serve as diagnostic characteristics of subfamilial or familial classifications.

The Ceratophryinae occurs over much of South America east of the Andes and south to the Chacoan region of Argentina. *Ceratophrys stolzmanni* occurs in the arid region of Pacific Ecuador and adjacent Peru, and one or two species of the genus inhabit the Carib-

bean versant of the Guyana massif and the Santa Marta Range of Colombia.

Ceratophrys Wied, 1824
(Figs. 74-75)

Phrynocerus Rafinesque, 1815, Anal. Nat., p. 78 [*Nomen nudum*].

Ceratophrys Wied, 1824, Isis (Oken), 1824: 672 [Type-species by monotypy, *Ceratophrys varius* Wied, 1824].

Stombus Gravenhorst, 1825, Isis (Oken), 1825: 920 [Type-species by present designation, *Rana cornuta* Linné, 1758].

Phrynoceros Bibron *in* Tschudi, 1838, Classif. Batr., p. 82 [Type-species by monotypy, *Phrynoceros vaillanti* Bibron, 1838].

Trigonophrys Hallowell, 1856, Proc. Acad. Nat. Sci. Philadelphia, 8:298 [Type-species by monotypy, *Trigonophrys rugiceps* Hallowell, 1856].

Chacophrys Reig and Limeses, 1963, Physis, 24:125 [Type-species by original designation, *Ceratophrys pierotti* Vellard, 1948].

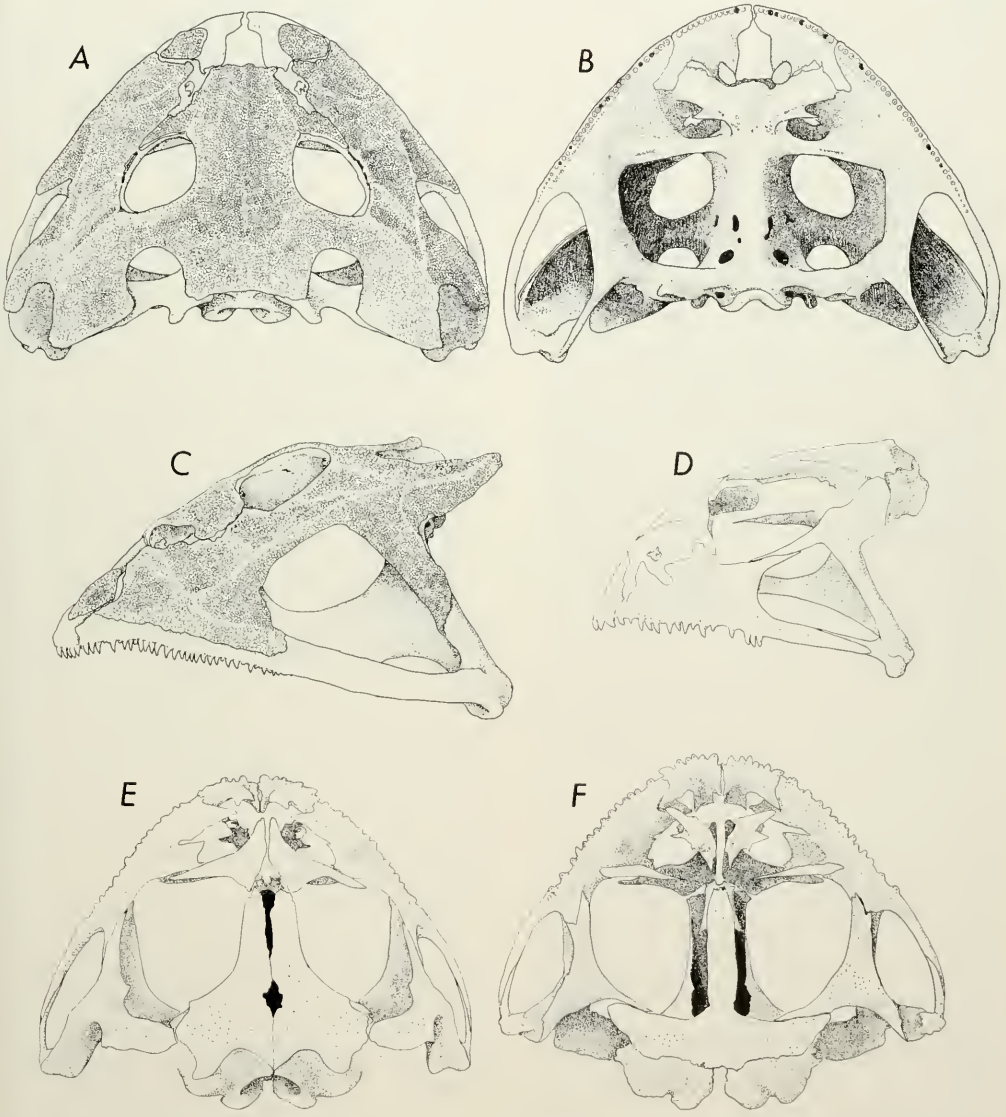

FIGURE 74. (A-C) dorsal, ventral, and lateral views of skull of an adult *Ceratophrys aurita* (KU 98129, × 1). (D-F) lateral, dorsal, and ventral views of skull of a post-metamorphic (stage 46) *C. ornata* (UMMZ 109753, × 2.5).

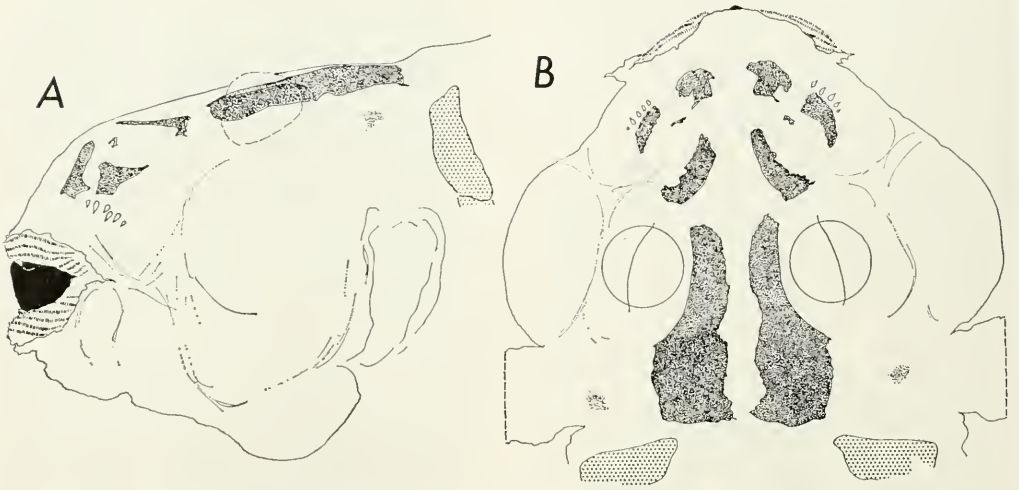

FIGURE 75. (A) lateral and (B) dorsal views of cleared and stained skull of a tadpole (Stage 41) of *Ceratophrys ornata* (UMMZ 98834, × 1.4).

Diagnostic definition.—7) omosternum very large; 10) alary processes of premaxillae directed posterodorsally, wide at base; 11) palatal shelf of premaxilla lacking; 12) facial lobe of maxilla very deep; 13) palatal shelf of maxilla not evident anteriorly, forming large pterygoid process posteriorly which is fused to pterygoid in adult; 15) nasals large, fused medially; 16) nasal fused to maxilla, nasal-pterygoid relationship not evident in adult; 17) nasals broadly fused to frontoparietals in adult; 21) temporal arcade forming supratemporal fenestrae, temporal arcade notched posteriorly; 22) epiotic eminences prominent, concealed dorsally by temporal arcade; 23) cristae paroticae long, narrow; carotid artery enclosed in dermostosed cranial bones; 24) zygomatic ramus of squamosal fused with squamosal process of maxilla, forming broad postorbital bar; 25) otic ramus of squamosal long, expanded medially into broad otic plate; 26) squamosal-maxillary angle 40-50°; 28) prevomers large, entire, toothed, fused to sphenethmoid; 29) palatines not distinguishable in adult, palatine area bearing large odontoids on odontoid ridge; 30) sphenethmoid entire in postmetamorphic specimens; 31) anterior ramus of parasphenoid narrow, long, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids large, no ventral flange, extent of anterior rami not evident in adults; 35) mandible bearing small odontoids at symphysis, relatively sharp odontoidal ridge along most of angular; 40) *m. depressor mandibulae* in two slips dorsally, ventrally in one large muscle block; 41) pupil horizontal; 42) males with median, subgular vocal sac; nuptial excresences on thumb; 43) body lacking glands; 44) tongue large, posterior edge free; 45) toes basally webbed, outer metatarsal tubercle present, inner metatarsal tubercle spadelike, digital tips narrow, first finger longer than second; 46) larval tooth rows 6/7, horny beak large; 49) adults 40-170 mm. SVL; 50) tympanum visible externally or concealed.

Composition.—The following nominal species are included in the genus: *aurita* (*dorsata* and *varia* are synonyms), *calcarata, cornuta, ornata, pierotti, stolzmanni,* and *testudo.* Dr. Oswaldo Reig is currently engaged in a revision of this genus.

Distribution.—South America east of the Andes and south to the Argentine Chaco; dry Pacific lowlands of Ecuador

and adjacent Peru; Santa Marta Mountains of Colombia; Caribbean slopes of Andes of Venezuela.

Remarks.—The skulls of adult *Ceratophrys* contain only three pairs of bones that are not fused into an akinetic mass, the columellae, premaxillae and septomaxillae. The septomaxillae are proportionately minute. The premaxillae of ceratophryines are unique in that the palatal shelf is lost (Fig. 11). In dry skeletons a calcified ball is often found lying behind the upper-most part of the alary process of the premaxilla; this ball apparently is formed from the alary cartilage. Some of the bones of the skull of *Ceratophrys* (nasals, frontoparietals, squamosals, and maxillae) are heavily encrusted with exostoic processes, and the suture lines are obliterated. The suture lines in the rest of the skull are not evident in adults, presumably owing to the extensive calcification of cartilage in the skull, and the concommitant fusion of all skull bones (except the columellae, premaxillae, and septomaxillae). In order to clarify the relationships of the topographic regions of the skull, an advanced tadpole (stage 41, *fide* Gosner, 1960) and a post-metamorphic specimen (stage 46) were cleared and stained. The tadpole (Fig. 75) is in an extremely advanced osteological condition for a bufonoid tadpole. The nasals, maxillae, premaxillae, and septomaxillae are relatively well developed, and teeth for the maxilla are evident. There is a small center of ossification in the area of the proötic.

The post-metamorphic specimen is likewise precociously developed osteologically (Fig. 74). The juvenile skeleton is described below, and the descriptive phrases are arranged in the same manner as a diagnostic definition. The description is based on UMMZ 109753. 1) sternum a cartilaginous plate; 2) vertebral shield absent; 3) transverse processes of anterior presacral vertebrae widely expanded; 4) cervical cotylar arrangement type III; 5) cervical and second vertebrae not fused; 6) cranial bones not involved in dermostosis; 7) omosternum large; 8) sacral diapophyses rounded; 9) maxillary arch toothed, teeth long, not pedicellate; 10) alary processes of premaxillae directed posterodorsally; 11) palatal shelf of premaxilla absent except for small palatal process; 12) facial lobe of maxilla deep, heavily exostosed; 13) palatal shelf of maxilla absent anteriorly, posteriorly represented by large pterygoid process; 14) maxillary arch complete, squamosal process large, completing squamosal-maxillary bridge; 15) nasals large, in broad median contact; 16) nasals in broad articular contact with maxillae, not contacting pterygoids; 17) nasals and frontoparietals in broad contact; 18) frontoparietal fontanelle very small; 19) frontoparietals exostosed, lacking crests; 20) frontoparietals not fused with proötics; 21) frontoparietals are expanded posterolaterally to cover median portion of cristae paroticae and form temporal arcade; supratemporal fenestrae present; 22) epiotic eminences prominent; 23) cristae paroticae long, slender; carotid artery enclosed in canal; 24) zygomatic ramus of squamosal elongate, forming upper half of squamosal-maxillary bridge; 25) otic ramus of squamosal large with large otic plate which is in contact with frontoparietal; 26) squamosal-maxillary angle 50°; 27) columella present; 28) prevomers relatively small, entire, separated medially, dentigerous processes lie posterior to choanae; 29) palatines long, separated medially; 30) sphenethmoid entire, not visible dorsally; 31) anterior ramus of parasphenoid long and narrow; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids moderate-sized, anterior rami long, not reaching palatines; 34) occipital condyles large, closely approximated, articular surfaces separate; 35) mandible lacking odontoids; 36) terminal phalanges knobbed. In

contrast to the adult condition, the septomaxillae are large.

The principal difficulty surrounding *Ceratophrys* has been the definition of and, consequently, the composition of, the genus. Few authors confused *Lepidobatrachus* or *Odontophrynus* with *Ceratophrys*, but many non-South American authors failed to perceive the many differences between *Ceratophrys* and the generic group currently referred to under the invalid generic name *Stombus* Gravenhorst, 1825.

Gravenhorst (1825) proposed the generic name *Stombus* and included three species in the genus (*Rana cornuta* Linné, *R. megastoma* Spix, and *R. scutata* Spix); he did not designate a type-species. He later (1829) published another paper with the combination *Stombus boiei*; most authors have cited this paper as the one in which the generic name was proposed and cite *boiei* as the type-species; Cope (1866) designated *boiei* as the type-species. South American herpetologists, unlike most European and North American herpetologists, have realized that the species similar to *Ceratophrys cornuta* are clearly generically distinguishable from those similar to *Stombus boiei*. However, the South American authors have used the invalid generic *Stombus* for this group. Of the three species originally included in *Stombus*, two (*cornuta* and *megastoma*) are conspecific and are members of the genus *Ceratophrys*; the third, *scutata*, is an older specific name for the type-species of a hylid genus, *Hemiphractus spixii* Wagler, 1828. Selection of the type-species of *Stombus* should depend on the avenue of least instability. If *scutata* is selected, then *Stombus* is the valid generic name for the hylid genus presently called *Hemiphractus*; if either *cornuta* or *megastoma* is selected, then *Stombus* is a synonym of *Ceratophrys*. In either case, the generic name for the group now called *Stombus* must change. The hylid generic name is entrenched in the literature, and any attempt to change it would promote instability. Therefore, *Rana cornuta* Linné, 1758, is selected as the type-species of *Stombus* Gravenhorst, 1825. The generic group previously called *Stombus* has only one primary synonym, *Proceratophrys* Miranda-Ribeiro, 1920, which is now the valid generic name (see pp. 133-34). *Ceratophrys* and *Proceratophrys* differ in the extent of the cranial bones, dermostosis of the cranial bones, presence of a vertebral shield, expansion of the transverse processes of the vertebrae, the development of supernumerary plantar tubercles, webbing of the toes, and tadpole morphology. *Proceratophrys* is a genus of the subfamily Telmatobiinae and the tribe Odontophrynini.

Reig and Limeses (1963) named *Chacophrys* for *Ceratophrys pierotti* and distinguished the genus from *Ceratophrys* solely by an assortment of characters reflecting the less extensive ossification of *pierotti*. The skeletal characteristics of *Chacophrys* are identical with those of the post-metamorphic (stage 46) *Ceratophrys ornata* (see fig. 74 and description on pp. 107-8). I am not recognizing *Chacophrys*, because its distinction rests on paedomorphic characters. The characters given by Vellard (1948) and Reig and Limeses (1963) for *pierotti* do not distinguish that taxon from juvenile *C. ornata*, but I recognize *pierotti* as a valid species, because José Cei assures me that it is different from *ornata*. Furthermore, the number of the chromosomes in the two species is strikingly different. I am not familiar with either species in the field.

Lepidobatrachus Budgett, 1899
(Fig. 76)

Lepidobatrachus Budgett, 1899, Quart. J. Micr. Sci., (2)42:329 [Type-species by present designation, *Lepidobatrachus asper* Budgett, 1899].

Diagnostic definition.—7) omosternum absent; 10) alary processes of premaxillae directed posterodorsally, long and narrow; 11) palatal shelf of pre-

maxilla lacking except for small palatal process; 12) facial lobe of maxilla deep, exostosed, in broad contact with nasal; 13) palatal shelf of maxilla lacking anteriorly, pterygoid process developed posteriorly; 15) nasals in median contact, small; 16) nasals in broad contact with maxillae, narrow contact with squamosals below eye, not in contact with pterygoids; 17) nasals in broad contact with frontoparietals; 21) supratemporal fenestrae absent, temporal notch absent; 22) epiotic eminences absent; 23) cristae paroticae broad; carotid artery enclosed in bony canal; 24) zygomatic ramus of squamosal contacting maxilla and nasal below eye; 25) otic ramus of squamosal short, but expanded medially into broad otic plate which covers crista parotica; 26) squamosal-maxillary angle 35-55°; 28) prevomers entire, toothed, separated medially, dentigerous processes situated between posterior borders of choanae; 29) palatines absent; 30) sphenethmoid entire, not visible dorsally; 31) anterior ramus of parasphenoid narrow, lacking median keel; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids massive, anterior rami not reaching palatine area; 35) mandible lacking odontoids; 40) *m. depressor mandibulae* in single slip—*pars tympanicus*; 41) pupil vertical; 42) males with median, subgular vocal sac, nuptial excrescences on thumb; 43) body lacking glands; 44) tongue large, posterior edge free; 45) toes two-thirds to three-fourths webbed, outer metatarsal tubercle lacking, inner metatarsal tubercle spade-like, digital tips narrow, first finger as long as second; 46) larvae lacking horny beak and denticles; 49) males 46-98, females 44-123 mm. SVL; 50) tympanum visible externally.

Composition.—Three species are recognized—*asper* (*salinicola* is a synonym), *laevis*, and *llanensis*. The genus was revised by Reig and Cei (1963) and Barrio (1968).

Distribution.—The Gran Chaco of Argentina and Paraguay.

Remarks.—Boulenger (1919) synonymized *Lepidobatrachus* with *Ceratophyrs*. With the discovery of the tadpole of *laevis*, Parker (1931) suggested that when the anatomy of the adult was more fully known, the genus *Lepidobatrachus* would be recognized. Most subsequent authors continued to use *Lepidobatrachus* as a valid generic name probably

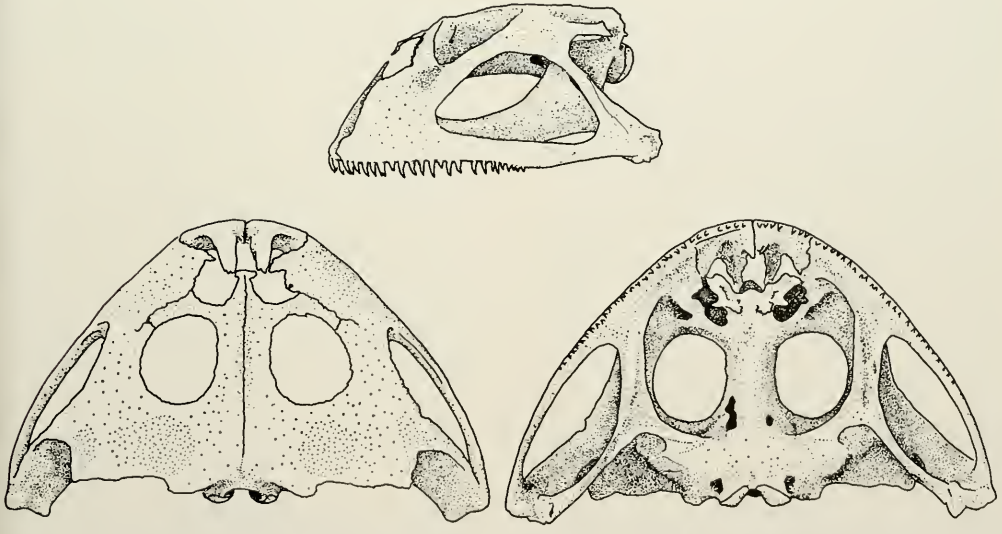

FIGURE 76. Lateral, dorsal, and ventral views of skull of *Lepidobatrachus asper* (KU 80783, × 2). No attempt was made to illustrate the dermosteotic pattern.

because Nieden (1923) recognized the genus. Nieden ceased to gather literature data in 1915 and publication of his work was delayed by World War I; it seems likely that he never saw Boulenger's (1919) paper. Subsequently adequate data have accumulated to substantiate the generic distinction of *Lepidobatrachus* (Reig, 1960b, Reig and Cei, 1963, and Cei, 1968a). *Lepidobatrachus* differs from *Ceratophrys* in having a vertical pupil, no outer metatarsal tubercle, greater webbing of the toes, no supratemporal fenestrae, and no horny beak or denticles in the larvae. Several published illustrations of *Lepidobatrachus* illustrate a more or less rhomboidal pupil (Cochran, 1961a, Reig and Cei, 1963), whereas others illustrate a vertical slit (Cei, 1955).

†Wawelia Casamiquela, 1963

Wawelia Casamiquela, 1963, Ameghiniana, 3: 144 [Type-species by original designation, *Wawelia gerholdi* Casamiquela, 1963].

Casamiquela (1963) named *Wawelia gerholdi* on the basis of a single, incomplete specimen of an Upper Miocene frog from Argentina. The fossil consists of a small piece of the dermostosed skull roof, parts of the pectoral girdle, the complete vertebral column, the left ilium, and left leg. Casamiquela placed the fossil in the Ceratophrydidae and considered it allied to *Ceratophrys*. Cei (1968a) considered *Wawelia* to be directly in the phyletic line of *Lepidobatrachus*, but presented no data supporting his conclusion.

The widely expanded transverse processes of the anterior presacral vertebrae of *Wawelia* are exactly like those of *Ceratophrys* and *Lepidobatrachus* (see Fig. 32). The characters evident on the ilium of *Wawelia* are not sufficiently diagnostic to separate the ilia of *Wawelia* and the other ceratophryines. The skull of *Wawelia* was not preserved; it is therefore not possible to tell if the fossil had a supratemporal fenestra. *Wawelia* is tentatively recognized as a valid genus, although it is not possible to distinguish the fossil from either *Ceratophrys* or *Lepidobatrachus*.

Telmatobiinae Fitzinger, 1843

Telmatobii Fitzinger, 1843:31.
Hylodidae Günther, 1859a:90.
Alsodina Mivart, 1869:290.
Cacotina Mivart, 1869:290.
Grypiscina Mivart, 1869:295.
Telmatobiidae: Miranda-Ribeiro, 1926:14.
Pseudinae (part): Noble, 1931:499.
Ceratophryinae (part): Parker, 1935:511.
Telmatobiinae Vellard, 1951:21.
Cyclorhamphinae Lutz, 1954:175.
Eleutherodactylinae Lutz, 1954:175.
Calyptocephalellinae Reig, 1960a:126.
Batrachylinae Gallardo, 1965:83.
Cycloramphinae: Gallardo, 1965:84.

The Telmatobiinae is the largest leptodactylid subfamily and contains one fossil and 24 Recent genera. I divide the Telmatobiinae into five tribes—Telmatobiini, Alsodini, Odontophrynini, Grypiscini, and Eleutherodactylini. The genera of the Telmatobiini and Alsodini are the most primitive of the Telmatobiinae and are distributed in temperate South America. These two tribes and the Odontophrynini exhibit orthodox breeding habits in that the eggs are laid in water (except *Batrachyla*), and an aquatic tadpole stage is present (all genera). In the more advanced genera (tribes Grypiscini and Eleutherodactylini) there is a decided tendency towards direct development.

The genera of the Telmatobiini and some of the genera of the Alsodini and Odontophrynini share several characters with the Cycloraninae and Heleophryninae: cervical cotylar arrangement type II, occipital condyles large and closely approximated, a tendency for the sacral diapophyses to be dilated, comparatively short transverse processes of the posterior presacral vertebrae (relative to those of the advanced genera), and heavy-boned skulls. In addition, two primitive non-osteological characters, which occur in many of the old World leptodactylids, are found in some of the genera of these tribes. These characters

are vertical pupils and the absence of outer metatarsal tubercles. The primitive Neotropical genera also have median vents in the tadpoles. The frogs of the Eleutherodactylini, the most successful tribe, range north through Central America and the West Indies to the southern United States. The diversity of morphology and biology of the genera of this subfamily is reflected in the few characters that are common to the 24 Recent genera. The following characteristics are consistent in all of the 24 genera of the Telmatobiinae: 1) sternum cartilaginous; 2) vertebral shield lacking; 3) transverse processes of anterior presacral vertebrae not widely expanded; 35) mandible lacking odontoids; 38) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 48) eggs laid in water, in terrestrial situations, or in bromeliads. When present, the maxillary teeth are blunt and pedicellate 9).

Telmatobiini Fitzinger, 1843

Telmatobii Fitzinger, 1843:31.
Telmatobiidae: Miranda-Ribeiro, 1926:14.
Telmatobiinae Vellard, 1951:21. Burger, 1954: 195-96. Gallardo, 1965:83.
Calyptocephalellinae Reig, 1960a:126.

The tribe Telmatobiini is used for five genera *(Batrachophrynus, Caudiverbera, Neoprocoela, Telmatobius,* and *Telmatobufo).* The group is distributed in the Andes from southern Ecuador to southern Chile, and in the lowlands of southern and central Chile. Oligocene and Miocene records of the group are known from central Argentina. At first glance, the group seems to be highly heterogeneous, but the genera can be arranged in a linear series in which the adjacent genera are more closely related to each other than to any non-adjacent genus: *Caudiverbera — Telmatobufo — Telmatobius — Neoprocoela — Batrachophrynus.*

The genera of the Telmatobiini share the following diagnostic characters which are not repeated in the generic accounts: 4) cervical cotylar arrangement type II; 14) maxillary arch complete; 20) frontoparietals not fused to proötics; 36) terminal phalanges knobbed; 42) males with nuptial asperities on thumb; some species of *Telmatobius* also have patches of small spines on the chest; 47) amplexus axillary; 48) eggs numerous, small, laid in gelatinous masses in ponds and sloughs. All genera of the tribe have massive and strongly curved clavicles (see Fig. 34) and large omosterna and sterna. The sternum tends to calcify in old adults of all of the genera.

Caudiverbera is the most divergent genus of the tribe and most of its unique characters are reflections of the casqued head. Unlike the other genera of the tribe, *Caudiverbera* lacks a frontoparietal fontanelle and has a large otic plate on the squamosal.

Fitzinger (1843) included *Telmatobius* in this family group. Vellard (1951) and Gallardo (1962) included only *Batrachophrynus* and *Telmatobius.* Gallardo (1962) considered *Telmatobufo* a synonym of *Aruncus* and most closely related to *Caudiverbera.* Schmidt (1952) suggested that *Telmatobufo* was closely related to *Telmatobius.* Schaeffer (1949) considered the Oligocene *Neoprocoela* most closely allied to *Batrachophrynus* and *Telmatobius.* Tihen (1962b) erroneously synonymized *Neoprocoela* with *Bufo. Neoprocoela* is regarded by me as a direct ancestor to *Batrachophrynus.*

Barbour and Noble (1920) provided the current generic separation of *Cycloramphus* and *Telmatobius.* Earlier authors had confused the two genera and regarded them as very closely related (Boulenger, 1907, Miranda-Ribeiro, 1920). Because some species of *Cycloramphus* have extensive webbing of the toes and *Telmatobius* has fully webbed toes, many modern herpetologists regard them related. The differences between the two genera are so trenchant that I place them in different tribes. Osteologically, there is little in common be-

tween the two, and the only external characters in which they resemble one another are the amount of webbing of the toes (not all species of *Cycloramphus*) and horizontal pupils.

Caudiverbera Laurenti, 1768

(Figs. 77-78)

Caudiverbera Laurenti, 1768, Synop. Rept., p. 43 [Type-species by monotypy, *Caudiverbera peruviana* Laurenti, 1768 (=*Lacerta caudiverbera* Linné, 1758)].

Peltocephalus Bibron, *in* Tschudi, 1838, Classif. Batr., p. 81 [Type-species by monotypy, *Peltocephalus quoyii* Bibron, *in* Tschudi, 1838; preoccupied by *Peltocephalus* Duméril and Bibron, 1835 (Reptilia: Chelonia)].

Calyptocephalus Duméril and Bibron, 1841, Erpétologie généralé, 8:447 [Type-species by monotypy, *Calyptocephalus gayi* Duméril and Bibron, 1841; preoccupied by *Calyptocephalus* Gray, 1832 (Insecta: Coleoptera)].

Calyptocephala Nieden, 1923, Das Tierreich, 46:371 [Replacement name for *Calyptocephalus* Duméril and Bibron, 1841 (preoccupied) and hence taking same type-species; preoccupied by *Calyptocephala* Dejean, 1835 (Insecta: Coleoptera)].

Calyptocephalella Strand, 1928, Ark. Naturgesch., 92A:55 [Replacement name for *Calyptocephalus* Duméril and Bibron, 1841 (preoccupied) and for *Calyptocephala* Nieden, 1923 (preoccupied) and hence taking same type-species].

Eophractus Schaeffer, 1949, Bull. Amer. Mus. Nat. Hist., 93:49 [Type-species by original designation, *Eophractus casamayorensis* Schaeffer, 1949].

Gigantobatrachus Casamiquela, 1959, Rev. Asoc. Geol. Argentina, 13:174 [Type-species by original designation, *Gigantobatrachus parodii* Casamiquela, 1959].

Diagnostic definition.—3) transverse processes of anterior presacral vertebrae very slightly expanded, those of posterior presacral vertebrae somewhat shortened; 5) cervical and second vertebrae free; 6) cranial bones involved in extensive dermostosis; 7) omosternum very large; 8) sacral diapophyses dilated; 9) maxillary arch toothed, teeth elongate, pedicellate; 10) alary processes of premaxillae directed posterodorsally, relatively broad at base; 11) palatal shelf of premaxilla relatively broad, slightly indented, palatal process short; 12) facial lobe of maxilla deep, heavily exostosed; 13) palatal shelf of maxilla of moderate width, pterygoid process large; 15) nasals large, in broad median contact; 16) nasals in broad contact with maxillae, separated from pterygoids; 17) nasals in broad contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals exostosed, extensive denticulate ornamentation; 21) temporal arcade complete, not notched, su-

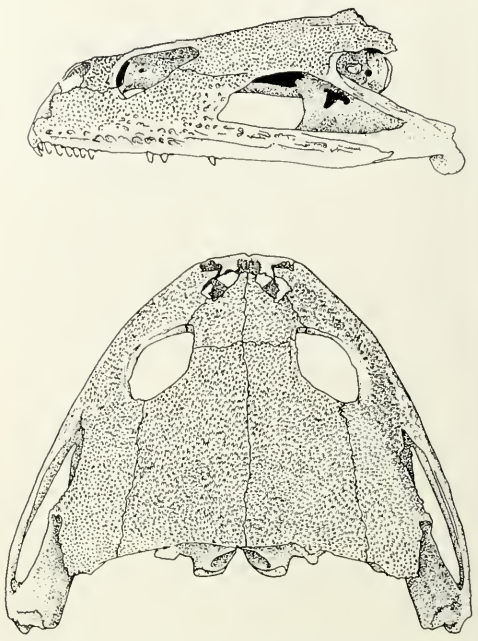

FIGURE 77. Lateral and dorsal views of skull of *Caudiverbera caudiverbera* (FMNH 9703, × 1).

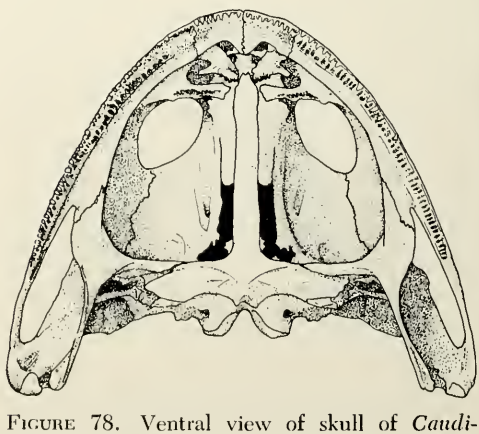

FIGURE 78. Ventral view of skull of *Caudiverbera caudiverbera* (FMNH 9703, × 1).

pratemporal fenestra absent; 22) epiotic eminences not apparent; 23) cristae paroticae broad and long; carotid artery enclosed in bony canal; 24) zygomatic ramus of squamosal large, in broad contact with squamosal process of maxillary forming complete post-orbital bridge; 25) otic ramus of squamosal large, expanded medially into broad otic plate which is in articular contact with frontoparietal; 26) squamosal-maxillary angle about 20° in adults, larger in juveniles; 27) columella present; 28) prevomers relatively small, entire, toothed, narrowly separated medially; 29) palatines broad, separated medially by width of parasphenoid, bearing numerous odontoids in large individuals; 30) sphenethmoid large, entire, extending anteriorly to middle of nasals, completely concealed dorsally by nasals and frontoparietals; 31) anterior ramus of parasphenoid long, narrow, not keeled, extending anteriorly between palatines to level of dentigerous processes of prevomers; 32) parasphenoid alae large, broad, oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively large, anterior rami not reaching palatines, small ventral flange on body of pterygoids; 34) occipital condyles large, narrowly separated medially; 37); 40); 41) pupil vertical; 42) male with median, subgular vocal sac; 43) body lacking glands; 44) tongue large, circular, not notched, posterior edge free; 45) toes three-fourths webbed, outer metatarsal tubercle lacking, inner metatarsal tubercle not spade-like, digital tips narrow, first finger as long as second; 46) larvae with median vent, 3/3 tooth rows, labial papillae interrupted anteriorly; 49) adults usually 80-220 mm. SVL; fossils are known to reach a length of more than 300 mm. SVL; 50) tympanum visible externally.

Composition.—One Recent and one fossil species are recognized here. Eleven names have been proposed for the single Recent species: *caudiverbera* Linné, 1758, *peruviana* Laurenti, 1768, *cristatus* Daudin, 1802, *feuillaei* Duméril and Bibron, 1836, *quoyii* Bibron, 1838, *gayi* Duméril and Bibron, 1841, *ater* Philippi, 1902, *coxi* Philippi, 1902, *rufa* Philippi, 1902, *canqueli* Schaeffer, 1949, and *parodii* Casamiquela, 1959. The last two names were proposed for Oligocene and Miocene fossils respectively. *Eophractus casamayorensis* Schaeffer is tentatively recognized as a valid species of *Caudiverbera* although it bears striking resemblance to the types of *Gigantobatrachus parodii. Caudiverbera casamayorensis* is known only from the Lower Eocene of Chubut, Argentina. Fossils that are assignable to the Recent species are known from the Upper Oligocene and Middle and Upper Miocene of Chubut, Rio Negro, and Santa Cruz, Argentina.

Distribution.—In Recent times, the species is known from localities in Chile between 30° and 42° S latitude. The fossils are known from central Argentina.

Remarks.—Myers (1962) pointed out that the correct generic and specific name for this large Chilean frog was *Caudiverbera caudiverbera.* Cei (1962a) and Gorham (1966) objected to this usage, arguing that *Calyptocephalella* should be used to promote stability. When "stability" is used as an argument for preserving or rejecting a name, some effort should be made to document the implied statement that this name or that name has been more frequently used. Because the species is restricted in distribution, relatively little literature on it has accumulated in the past 50 years. The majority of "name usages" for the species are simple inclusions in lists of one sort or another. Such usages are not, in my opinion, equal in weight to a discussion of biology, systematics, or nomenclature. Fewer than a half-dozen significant papers have appeared in the last 50 years treating this species; in these, the generic names used were *Calyptocephala, Calyptocephalella,* and *Caudiverbera.* Thus, an argument based

on "stability" is capricious. Myers' (1962) arguments are irrefutable; *Caudiverbera* is here used as the valid generic name, and Linné's *caudiverbera* is used in preference to Duméril and Bibron's *gayi*.

Eophractus and *Gigantobatrachus* are here placed in the synonymy of *Caudiverbera* for the first time. Both genera were separated from *Caudiverbera* on the basis of dermostoic patterns, and *Gigantobatrachus* further separated on the basis of size. *Eophractus* was diagnosed, in part, on the presence of a shallow groove on the maxilla. This groove is present in the largest specimen of *Caudiverbera* that I have examined, but not in the four smaller specimens. In the larger specimens of *Caudiverbera*, the denticles of bone on the skull begin to fuse to adjacent denticles. In both *Eophractus* and *Gigantobatrachus*, the exostosed bones have a dermosotic pattern in which the bone appears pitted. The pitting is a result of fusion of adjacent denticles. I consider these characters to be due to age difference and therefore not applicable to generic separation. Young specimens of the Recent population have pitted dorsal surfaces of the exostosed bones.

The skull of *Caudiverbera* is superficially similar to those of the ceratophryines, but differs in the forward shift of the eyes, pedicellate teeth, and the presence of well defined sutures. The vertebral column of *Caudiverbera* differs from those of the ceratophryines in having non-expanded transverse processes of the anterior presacral vertebrae, in lacking a dermostosed vertebral shield, and in having dilated sacral diapophyses. The vertebral column of *Caudiverbera* is more similar to that of *Telmatobufo* than to those of the other genera of the tribe. As in the other Telmatobiini, the pectoral girdle is massive with strongly arched and massive clavicles and has a large omosternum and large sternum (Fig. 34).

Reig (1960a) placed *Calyptocephalella* (=*Caudiverbera*) in a separate subfamily Calyptocephalellinae. The separation was based on the peculiarities of the skull of *Caudiverbera*. However, *Caudiverbera* shares many osteological, external, and non-osteological characters with *Batrachophrynus*, *Telmatobius*, and *Telmatobufo*, and differs from them in having a completely roofed skull and the skin of the head involved in dermostosis with the skull bones. Reig (1960a) did not compare *Caudiverbera* with *Telmatobufo*, and therefore was unaware of the numerous similarities between them. *Telmatobufo* is intermediate between *Caudiverbera* and *Telmatobius* in many of the distinguishing characters of Reig's Calyptocephalellinae.

Telmatobufo Schmidt, 1952

Telmatobufo Schmidt, 1952, Fieldiana, Zool., 34:11 [Type-species by original designation, *Telmatobufo bullocki* Schmidt, 1952].

Diagnostic definition.—3) transverse processes of posterior presacral vertebrae shortened; 5) cervical and second vertebrae apparently fused; 6) cranial bones not involved in dermostosis; 7) omosternum very large; 8) sacral diapophyses dilated; 9) maxillary arch toothed, teeth pointed, slightly elongated, pedicellate; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla broad, apparently notched; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla relatively broad, pterygoid process lacking or poorly defined; 15) nasals not in median contact, relatively small; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle small; 19) frontoparietals not ornamented; 20); 21) temporal arcade lacking; 22) epiotic eminences poorly defined; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal of moderate length, pointed; 25) otic ramus of squamosal very short, not expanded to form otic plate; 26); 27) columella apparently ab-

sent; 28) prevomers small, entire, separated medially, bearing teeth; 29) palatines relatively narrow, long, separated medially, lacking odontoid ridge; 30) sphenethmoid entire, extending anteriorly to posterior edge of nasals; 31); 32) parasphenoid alae not overlapped by median rami of pterygoids; 33) anterior rami of pterygoids in long contact with maxillae, extending to palatines; 34) occipital condyles large, not stalked, closely juxtaposed; 37-39); 40) *pars scapularis* of *m. depressor mandibulae* minute, confined to a few muscle slips, *pars tympanicus* massive; 41) pupil vertical; 42) males apparently lacking nuptial asperities and vocal sac; 43) distinct parotoid glands present; 44) tongue large, rounded, posterior edge free; 45) toes fully webbed, outer metatarsal tubercle lacking, inner metatarsal tubercle not spade-like, digital tips narrow, first finger shorter than second; 46-48)[6]; 49) two adults examined were 63 and 64 mm. SVL; 50) tympanum absent; 51) fifth toe very broad, much broader than in any other leptodactylid.

Composition.—Monotypic.

Distribution.—Known only from the Cordillera de Nahuelbuta, Mallew, Chile.

Remarks.—The osteological characters (nos. 1-38) of *Telmatobufo bullocki* were studied by use of stereoradiographs of the holotype and paratype. The observation of some characteristics is very difficult and the statements listed above are subject to reinterpretation. For example, the first two vertebrae appear to be fused; this may not be the case, but judging from prior experience with skeletons and radiographs, I feel the present interpretation is probably correct. Similar arguments and qualifications can be made for several other characteristics involving skull bones. The transverse process of the posterior presacral vertebrae of *Telmatobufo* are shortened as in *Caudiverbera, Ceratophrys, Proceratophrys,* and a few other Neotropical leptodactylid genera. Except for the dilated sacral diapophyses, the vertebral column of *Telmatobufo* looks like that of *Proceratophrys* (Fig. 79). I consider *Telmatobufo* to be more closely related to *Caudiverbera* than to the other Telmatobiini. *Caudiverbera* and *Telmatobufo* share three characters which are not exhibited by the other Telmatobiini: shortened transverse processes of the posterior presacral vertebrae, vertical pupil, and absence of an outer metatarsal tubercle. The two genera differ in the casquing of the skull of *Caudiverbera*; the skull of *Telmatobufo* is identical, insofar as my observations will permit, with that of *Telmatobius.* In several respects *Telmatobufo* is intermediate between *Neoprocoela* and *Telmatobius* and fits the generalized pattern of Telmatobiini.

Schmidt (1952) suggested that *Telmatobufo* was closely allied to, but noticeably distinct from, *Telmatobius.* The only subsequent author to discuss the validity and relationships of *Telmatobufo* was Gallardo (1962, 1965), who suggested that *Telmatobufo bullocki* was identical with *Aruncus valdivianus* Philippi. He further suggested (1962) that *Aruncus* was not related to *Telmatobius* but to *Calyptocephalella (=Caudiverbera)* but did not substantiate his opinions with data.

Cei's (1958) reproductions of the long-lost and unpublished plates for Philippi's (1902) work provide much more evidence concerning the identities of the myriad of names proposed by Philippi than do Philippi's brief descriptions. The plates provide adequate grounds for rejecting Gallardo's contention that *Telmatobufo* Schmidt is a synonym of *Aruncus* Philippi. The plate for *Aruncus valdivianus* (plate I in Cei, 1958) indicates that the frog had little,

[6] A second species of *Telmatobufo* and larvae are being described by Ramón Formas Cortes. The genus has stream-adapted larvae with a tooth row formula of 2/3, a ventral mouth suggestive of that in *Ascaphus, Heleophryne,* and *Stauvois,* and papillae completely surrounding the mouth.

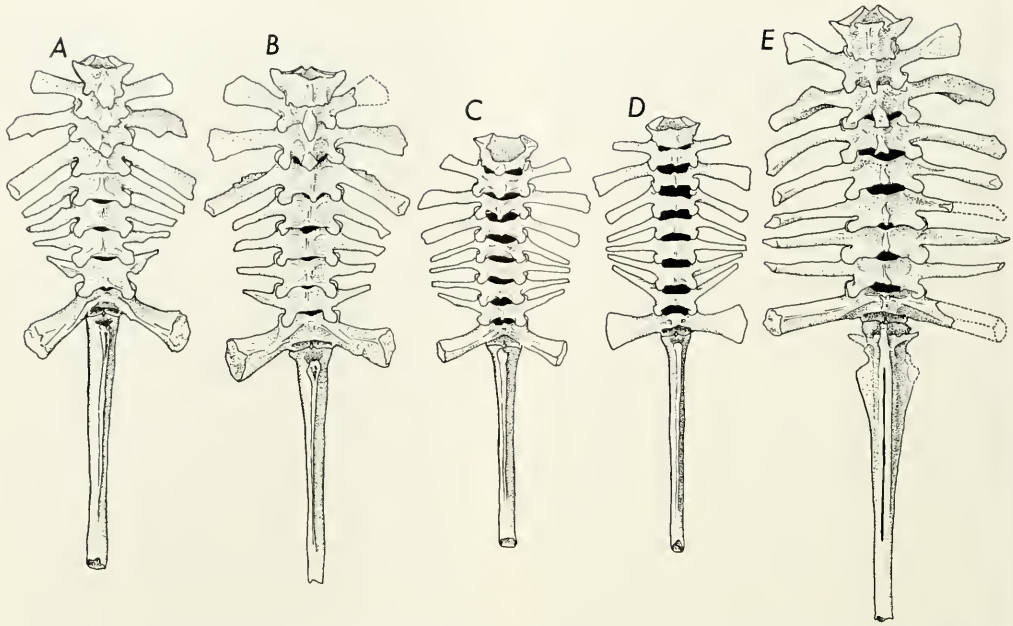

FIGURE 79. Vertebral columns of five genera of the Telmatobiinae. (A) *Proceratophrys cristiceps* (KU 106273, × 2), (B) *Odontophrynus cultripes* (KU 92975, × 2), (C) *Cycloramphus pinderi* (KU 92807, × 2), (D) *Thoropa miliaris* (KU 92856, × 2), and (E) *Batrachophrynus macrostomus* (KU 96127, × 1).

if any, webbing between the toes, whereas the specimens of *Telmatobufo bullocki* have fully webbed feet. The fingers of *Aruncus* are proportionately much longer than is the case for *Telmatobufo*. However, the most convincing data is the illustrated tympanum in *Aruncus valdivianus* and the absence of the tympanum in *Telmatobufo bullocki*. Cei's (1958) suggestion that the figures of *Aruncus valdivianus* represent a poor rendition of *Bufo spinulosus* is reasonable. Cei (1958) objected to the inclusion of *Aruncus valdivianus* in the synonymy of *Bufo spinulosus* because the figures are not sufficiently accurate to permit an assignment to subspecies, and the synonymy would affect the application of subspecific names. I suggest that *Aruncus valdivianus* Philippi, 1902, be considered a *nomen dubium* for the present.

Telmatobius Wiegmann, 1835
(Figs. 80-81)

Telmatobius Wiegmann, 1835, Nova Acta Acad. Leop.-carol, 17:262 [Type-species by monotypy, *Telmatobius peruvianus* Wiegmann, 1835].

Pseudobatrachus Peters, 1873, Mtber. k. Preuss. Akad. Wiss., Berlin, p. 414 [Type-species by monotypy, *Pseudobatrachus jelskii* Peters, 1873].

Cophaeus Cope, 1889, Bull. U.S. Natl. Mus., 34:312, 381 [Apparently a replacement or substitute name for part or all of Boulenger's (1882) *Telmatobius*, which Cope considered not equal to *Telmatobius* of Wiegmann (1835)].

Diagnostic definition.—3) transverse processes of posterior presacral vertebrae not shortened; 5) cervical and second vertebrae not fused; 6) cranial bones not involved in dermostosis; 7) omosternum large; 8) sacral diapophyses dilated; 9) maxillary arch toothed, teeth pointed, pedicellate; maxillary arch toothless in a few populations; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla narrow with relatively long palatal process; 12) facial lobe of maxilla relatively deep, not exostosed; 13) palatal shelf of maxilla relatively narrow, pterygoid process lacking; 14) maxillary

FIGURE 80. Dorsal and ventral views of skull of *Telmatobius hautholi* (KU 72879, × 5). Right septomaxilla lost in preparation.

arch complete in most species, quadratojugal lacking in edentulous *patagonicus*; 15) nasals separated medially and small in dentate species, larger and narrowly separated in *patagonicus*; 16) nasals not in contact with maxillae or pterygoids; 17) nasals widely separated from frontoparietals; 18) frontoparietal fontanelle small, except in *patagonicus* in which it is large; 19) frontoparietals not or but slightly ornamented; 21) temporal arcade absent; 22) epiotic eminences well defined; 23) cristae paroticae short and stocky; carotid artery not enclosed in a canal, sometimes a shallow groove is present on the frontoparietal and otoccipital; 24) zygomatic ramus of squamosal relatively long, blunt, widely separated from maxilla; 25) otic ramus of squamosal very short, no otic plate; 26) squamosal-maxillary angle about 40°; 27) columella present, absent in *patagonicus*; 28) provomers present, usually toothed, sometimes edentate, entire, in contact medially or narrowly separated; 29) palatines long and narrow, narrowly separated medially; 30) sphenethmoid entire, extending anteriorly to posterior edge of nasals; 31) anterior ramus of parasphenoid relatively narrow, lacking median keel, extending anteriorly between palatines; 32) parasphenoid alae oriented at right angles to anterior ramus, not overlapped laterally by median rami of pterygoids; 33) pterygoids relatively small, anterior rami elongate, nearly reaching palatines; 34) occipital condyles relatively large, not stalked, narrowly separated medially; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males lacking vocal sac; nuptial asperities or clusters of spines on thumb and sometimes on chest; 43) body lacking glands; 44) tongue large, rounded, posterior edge free; 45) toes usually completely webbed, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged, digital tips narrow; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae interrupted anteriorly; 49) adults to about 60 mm. SVL; 50) tympanum small or concealed.

Composition.—Vellard (1951) recognized 19 species of the genus. Schmidt

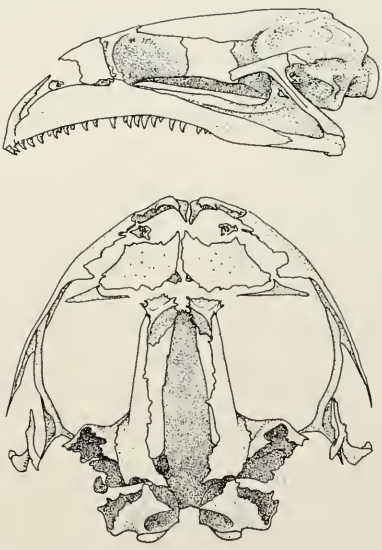

FIGURE 81. Lateral view of skull of *Telmatobius marmoratus* (UMMZ 68179, × 4) and dorsal view of skull of *Telmatobius patagonicus* (KU 80781, × 7.3).

(1954a) recognized 21 and Vellard (1960) modified his earlier account and recognized 23 species. *Batrachophrynus patagonicus* is a species of *Telmatobius* and one additional species has been described since Vellard's last paper. Fifty-one populations of *Telmatobius* are presently afforded nomenclatorial recognition. The following species of *Telmatobius* are recognized; the number of subspecies is included in parentheses: *albiventris* (4), *arequipensis* (2), *atacamensis*, *brevipes*, *brevirostris* (3), *cinereus*, *crawfordi* (2), *culeus* (6), *halli* (2), *hauthali* (2), *ignavus*, *intermedius*, *jelskii* (4), *laevis*, *marmoratus* (7), *montanus*, *niger*, *oxycephalus*, *patagonicus*, *peruvianus*, *praebasalticus*, *reverberii*, *rimac* (2), *simonsi*, *somuncurensis*, *vellardi*, and *verrucosus*.[7]

Distribution.—South American Andes from southern Ecuador (1° S) to central Chile and Argentina (32° S). The greatest diversity occurs in southern Peru.

Remarks.—As presently constituted, *Telmatobius* is one of the larger leptodactylid genera. Vellard (1951, 1953, 1955, 1960) placed the 23 species known to him in three species groups: *peruvianus* group (stream frogs), *marmoratus* group (primarily or totally aquatic frogs), and *jelskii* group (semiterrestrial frogs). However, several authors have pointed out that the closest relatives of some aquatic species are semiterrestrial species. Loss of the maxillary or prevomerine teeth has been a major taxonomic character in the study of the relationships of the frogs of this genus. Maxillary teeth are lost by some members of the *peruvianus* and *marmoratus* groups. Prevomerine teeth are lost by some populations of all species groups.

I have seen few skeletons of this genus, and therefore my characterization of it will probably undergo some alteration with the acquisition of additional material in the future. The paedomorphic *T. patagonicus* is strikingly different in cranial osteology (Fig. 81) from the other species I examined.

[7] The species list given here is incomplete. Cei and Vellard have increased the number of taxa known from Argentina. Gallardo (1970) and Cei *(in litt.)* suggest that *T. montanus* is more closely related to certain species here assigned to *Fupsophus*. Studies on the osteology of many species of *Telmatobius* are in progress and when completed should provide some clarification.

†Neoprocoela Schaeffer, 1949

Neoprocoela Schaeffer, 1949, Bull. Amer. Mus. Nat. Hist., 93:57 [Type-species by original designation, *Neoprocoela edentatus* Schaeffer, 1949 (=*N. edentata*), Lower Oligocene].

Schaeffer (1949) described and named a relatively well preserved bufonoid frog from the Lower Oligocene of Patagonia as a new genus and new species of Leptodactylidae. The fossil is edentate (as is reflected in Schaeffer's choice of a trivial name), has a moderately small frontoparietal fontanelle, and dilated sacral diapophyses. Schaeffer did not consider the fossil to be a bufonid because to do so ". . . would require the presence of the Bufonidae *(sensu stricto)* in South America by no later than the early Oligocene, an occurrence which is not supported by the known paleontological facts." Exactly what facts these were was not explained by Schaeffer. Instead, he assigned the fossil to the Leptodactylidae, and characterized it as having a number of primitive, criniid-like traits. Schaeffer suggested that *Neoprocoela* was related to *Batrachophrynus* and *Telmatobius*.

The discovery of a Miocene toad *(Bufo marinus)* from Colombia (Estes and Wassersug, 1963) clearly establishes the Bufonidae in South America from at least the Eocene because South America was isolated from Middle America between the Eocene and Pliocene (Lloyd, 1963). Therefore, Schaeffer's objections to placing *Neoprocoela* in the Bufonidae can be seriously questioned. Tihen (1962b) placed *Neoprocoela* in the synonymy of *Bufo* and considered the type-species as a species of the *B. calamita* group. Tihen associated the fossil with

Bufo for the following reasons: 1) in edentulous leptodactylids, the prevomers are greatly reduced in size, 2) the alary processes of leptodactylids are directed dorsally or laterally, not toward the midline as in *Neoprocoela edentata* and bufonids, 3) the sphenethmoid is entire in *Neoprocoela*, 4) the shape of the squamosal suggests a large squamosal-maxillary angle, 5) the broad nasals are in median contact, 6) there is a long maxillary-pterygoid contact, 7) the maxillae are very broad, 8) the atlantal cotyles are closely approximated ventrally, 9) the first transverse processes are directed anterolaterally and are expanded (=dilated), and 10) the sacral diapophyses are expanded (=dilated). Tihen cited two other characters of *Neoprocoela* which are uncommon in bufonids but characteristic of the *Bufo calamita* group —large frontoparietal fontanelle and very short otic ramus of the squamosal. Tihen argued that while each of the ten characteristics listed above can be demonstrated to occur in one or more leptodactylid groups, the simultaneous occurrence of all ten is not known for any leptodactylid, but is the case in *Bufo*. Tihen's "leptodactylid condition" for his comparison of *Neoprocoela*, leptodactylids, and bufonids, must have been based on the skeletons of some of the Australo-Papuan leptodactylids. Characters 3) and 5) of *Neoporcoela* are very much unlike the conditions seen in edentulous Australo-Papuan leptodactylids, but are like the conditions seen in some edentulous Neotropical leptodactylids. With the exception of characters 1), 2), and 10), *Neoprocoela* agrees completely with *Batrachophrynus*. The fossil agrees with *Batrachophrynus* in the two characteristics cited by Tihen that are "unusual" for *Bufo*. The dilation of the sacral diapophyses of *Neoprocoela* is not as great as in *Bufo*. The sacral diapophyses are round in *Batrachophrynus* (Fig. 79). The dilation of the sacral diapophyses of *Neoprocoela* is no greater than that seen in *Telmatobufo*, a close relative of *Batrachophrynus*. The length of the transverse processes of the posterior presacral vertebrae is not evident in the single fossil of *Neoprocoela*; this character is very different in *Batrachophrynus* and the *Bufo calamita* group.

Tihen recorded the alary processes (ascending processes of Tihen) of the premaxillae as directed toward the midline in *Neoprocoela*. This is not a leptodactylid trait but clearly a bufonid trait. Perusal of Schaeffer's figures clearly indicates that the skull of *Neoprocoela* was crushed and distorted. The skull apparently was crushed from the left to the right side. The premaxillae are distorted with an anterior rotation at their median suture; this results in a deflection toward the midline of the alary processes. As in *Batrachophrynus*, the alary processes are long and thin.

The large prevomers of *Neoprocoela* readily distinguish it from *Batrachophrynus*, in which the prevomers are minute. In *Caudiverbera*, *Telmatobius*, and *Telmatobufo*, the prevomers are large and toothed. It is only logical to assume that the ancestral stock of *Batrachophrynus* had large and toothed prevomers. In the course of loss of the prevomers and prevomerine teeth, two patterns are observed. In one pattern, tooth loss occurs late; the prevomerine bones are reduced in size until only the dentigerous ramus and a small semicircle of bone surrounding the inner edge of the choana remains. The teeth and dentigerous ramus are then lost, in that order. This is the pattern seen in the Myobatrachinae. In the other pattern, the prevomer is not greatly reduced in size before the teeth are lost. The bone continues to be reduced in size subsequent to tooth loss. This pattern is seen in several genera of the Telmatobiinae, Leptodactylinae, and Elosiinae. *Neoprocoela* fits the intermediate condition between *Telmatobufo* and *Batrachophrynus*.

Neoprocoela is intermediate between *Telmatobufo* and *Batrachophrynus* in

the shape of the sacral diapophyses and in shape of the cristae paroticae, as well as the size of the prevomers. Tihen also cited the "toad-like" body shape of *Neoprocoela* as an additional bufonid character. However, *Telmatobufo* is very toad-like even in the possession of well defined parotoid glands.

Based on the skeletal data evident in the figures of *Neoprocoela* published by Schaeffer (1949) and Tihen (1962b), the following characteristics of my diagnostic definition can be stated: 2) vertebral shield probably absent; 4) cervical cotylar arrangement type II; 5) cervical and second vertebrae not fused; 6) skull bones not exostosed, therefore derm of head free; 8) sacral diapophyses dilated; 9) maxillary arch edentate; 10) alary processes of premaxilla narrow, directed posterodorsally; 11) palatal shelf of premaxilla very broad, slightly indented; 12) facial lobe of maxilla deep; 13) palatal shelf of maxilla broad with a well developed pterygoid process; 14) maxillary arch complete; 15) nasals large, in broad median contact; 16) nasals in contact with maxillae; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle of moderate size; 19) frontoparietals not ornamented; 21) temporal arcade lacking; 23) cristae paroticae moderately short, stocky; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal very small, no otic plate; 28) prevomers large, edentate; 29) palatines elongate; 30) sphenethmoid large, entire; 32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid; 33) anterior rami of pterygoids elongate, in long contact with maxillae, reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 36) terminal phalanx of one digit knobbed; 49) snout-coccyx length at least 66 mm. The single terminal phalanx could be of the thumb even if the frog had T-shaped terminal phalanges.

Batrachophrynus Peters, 1873
(Fig. 82)

Batrachophrynus Peters, 1873, Mtber. k. Preuss. Akad. Wiss., Berlin [Type-species by present designation, *Batrachophrynus macrostomus* Peters, 1873].

Diagnostic definition.—3) transverse processes of posterior presacral vertebrae oriented at right angles to sagittal line, as long as sacral diapophyses; 5) cervical and second vertebrae not fused; 6) cranial bones not dermostosed; 7) omosternum present, large; 8) sacral diapophyses round; 9) maxillary arch edentate; 10) alary processes of premaxillae narrow, directed posterodorsally; 11) palatal shelf of premaxilla very broad, slightly indented; 12) facial lobe of maxilla deep; 13) palatal shelf of premaxilla broad, pterygoid process relatively small; 15) nasals large, in broad median contact; 16) nasals in contact with maxillae and pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle small; 19) frontoparietals not ornamented, except for a sharp shelf immediately posterior to orbit; 21) temporal arcade lacking; 22) epiotic eminences large posteriorly, obsolete anteriorly; 23) cristae paroticae very long and narrow; carotid artery not enclosed in bony canal, frontoparietals sometimes having groove between ridge and epiotic

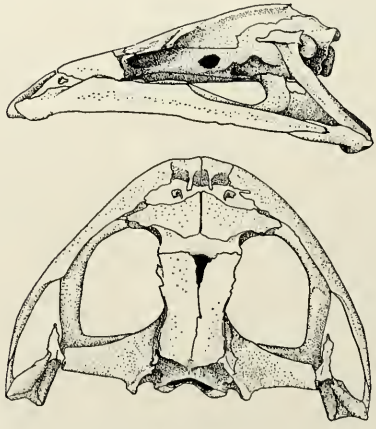

FIGURE 82. Lateral (× 1) and dorsal (× 0.7) views of skull of *Batrachophrynus macrostomus* (KU 96127).

eminence; 24) zygomatic ramus of squamosal short; 25) otic ramus of squamosal very short, no otic plate; 26) squamosal-maxillary angle 35-40°; 27) columella present, thin; 28) prevomers small, edentate, only dentigerous ramus present; 29) palatines broad, widely separated medially, lacking odontoids; 30) sphenethmoid large, entire, extending anteriorly to front of nasals; 31) anterior ramus of parasphenoid broad, pointed, keeled medially, extending anteriorly between palatines; 32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids very large, anterior rami in long contact with maxillae, reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males apparently lacking nuptial asperities and vocal sac; 43) body lacking glands; 44) tongue large, completely adherent; 45) toes fully webbed, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged, digital tips narrow, first finger longer than second; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae interrupted anteriorly; 49) adult *brachydactylus* are 47-58 mm. SVL and *macrostomus* grows to 160 mm. SVL; 50) tympanum absent.

Composition.—Two species are recognized, *brachydactylus* and *macrostomus*.

Distribution.—Lago de Junín region in central Peru.

Remarks.—*Batrachophrynus* and *Telmatobius* are usually considered to be very closely related and were separated solely on the basis of the presence *(Telmatobius)* or absence *(Batrachophrynus)* of maxillary and prevomerine teeth. Four populations of *Telmatobius* lack maxillary teeth *(brevipalmatus, edentatus, intermedius,* and *patagonicus)*. The palatal shelf is broad in *Batrachophrynus* and narrow in *Telmatobius*, the prevomers are small and edentate in *Batrachophrynus* but usually are moderate-sized to large and toothed in *Telmatobius* regardless of whether there are teeth on the maxillary arch, and the posterior edge of the tongue is not free in *Batrachophrynus*. The distinctions between *Batrachophrynus* and *Telmatobius* are difficult to assess at present because so few species have been studied. The aquatic *Telmatobius* bear greater resemblance in external characters to *Batrachophrynus* than to the semiterrestrial species of *Telmatobius*.

Alsodini Mivart, 1869[8]

Alsodina Mivart, 1869:290.
Cacotina Mivart, 1869:290.
Batrachylinae Gallardo, 1965:83.

Four genera are included in this Neotropical tribe—*Batrachyla, Eupsophus, Hylorina,* and *Thoropa*. The distribution of the group is only slightly more extensive than that of the Telmatobiini, in that one genus *(Thoropa)* is found in the mountains of southeastern Brasil. *Eupsophus* and *Hylorina* are closely related as are *Batrachyla* and *Thoropa*. However, the two generic pairs share few significant characters.[9] The cervical cotylar arrangement is type II in *Eupsophus* and *Hylorina*, whereas it is type I in *Batrachyla* and *Thoropa*.

[8] Barrio's (1970) *Insuetophrynus* probably belongs here but until specimens have been examined for all characteristics employed here (especially osteological), any assignment must be considered tenuous. Barrio considered the genus most closely allied to *Alsodes* (=*Eupsophus nodosus* group as used here) principally on the basis of the secondary sex characteristics. Further comment on *Insuetophrynus* is postponed pending completion of studies of the skeletons of *Eupsophus, Insuetophrynus,* and *Telmatobius*.

[9] In a separate paper (Lynch, MS) I used Batrachylini as the tribe name for *Batrachyla* and *Thoropa* and assigned *Eupsophus* and *Hylorina* to the Telmatobiini. This action reflects my incomplete knowledge of *Telmatobius* skeletons at present. I regard either arrangement as defensible at present and hope to clarify the relationships of these genera once my study of *Telmatobius* osteology is completed.

All four genera have frontoparietal fontanelles, vertebral columns in which the transverse processes of all vertebrae (except 1 and 2) are as long as the sacral diapophyses, and slightly dilated sacral diapophyses. All four genera have free swimming tadpoles. The tadpoles of *Batrachyla* differ from those of the other genera in having an uninterrupted series of labial papillae. The tadpoles of *Thoropa* are greatly flattened and attenuate (Fig. 2) in an adaptation to torrential stream life. Amplexus is inguinal in *Batrachyla*, but is axillary in *Eupsophus* and *Hylorina*; the amplectic position is not known for *Thoropa*. *Eupsophus* and *Hylorina* lay numerous small eggs in water, whereas *Batrachyla* lays fewer larger eggs in terrestrial sites. The eggs of *Batrachyla* hatch and the larvae live in the jelly mass until the mass is inundated. *Thoropa* has large eggs which are deposited on wet stones in situations where water trickles over stone ledges (Myers, 1946). Werner C. A. Bokermann (pers. comm.) suggested that the eggs are laid on the banks of the torrential streams inhabited by *Thoropa*.

The following diagnostic characteristics are uniform among the four genera of the group: 3) transverse processes of posterior presacral vertebrae long; 5) cervical and second vertebrae not fused; 6) cranial bones not involved in dermostosis; 7) omosternum present, moderately large; 8) sacral diapophyses somewhat dilated—see Fig. 79; 9) maxillary arch toothed, teeth blunt, pedicellate; 12) facial lobe of maxilla deep, not exostosed; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle moderate-sized; 19) frontoparietals not ornamented; 20) frontoparietal not fused with proötic; 21) temporal arcade lacking; 37) alary processes of hyoid plate on narrow stalks; 42) males with nuptial asperities on thumb and sometimes second finger; some species of *Eupsophus* have cluster of asperities on chest; 45) outer metatarsal tubercle present, inner metatarsal tubercle not enlarged or spade-like; 46) larvae with median vent.

The tribal name, Alsodini, is based on *Alsodes* Bell, 1843, which was recently shown to be a synonym of *Eupsophus* (Lynch, 1968b). The heterogeneity of the tribe and the mosaic of primitive characteristics exhibited by the four included genera suggest that the Alsodini might be best regarded as a suprageneric grade between the primitive Telmatobiini and the advanced Eleutherodactylini.

Eupsophus Fitzinger, 1843

(Fig. 83)

Eupsophus Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, *Cystignathus roseus* Duméril and Bibron, 1841].

Hammatodactylus Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, *Cystignathus nodosus* Duméril and Bibron, 1841].

Borborocoetes Bell, 1843, Zool. Voy. Beagle, Reptiles, 5:34 [Type-species by present designation, *Borborocoetes grayi* Bell, 1843; preoccupied by *Borborocoetes* Schoenherr, 1842 (Insecta: Coleoptera)].

Alsodes Bell, 1843, *Ibid.*, 5:34 [Type-species by monotypy, *Alsodes monticola* Bell, 1843].[10]

[10] Gallardo (1970) proposed recognizing *Alsodes* as distinct from *Eupsophus* and included seven Patagonian species in *Alsodes*. The seven are *Alsodes gargola* Gallardo, 1970, *Eupsophus illotus* (Barbour), 1922, *E. monticola* (Bell), 1843, *E. nodosus* (Duméril and Bibron), 1841, *Telmatobius montanus* Lataste, 1902, *T. praebasalticus* Cei and Roig, 1968, and *T. reverberii* Cei, 1969. Gallardo (1970) defined the genus *Alsodes* as follows: atlas convex, sternum expanded and notched posteriorly, tympanum not visible externally, vocal sac absent in males, forelimbs of reproductively active males greatly enlarged, and nuptial spines present on fingers and chest of reproductively active males. Barrio (1970) tentatively accepted Gallardo's arrangement but did not include *Telmatobius praebasalticus* and *T. reverberii* as species of *Alsodes*. Further comment on this arrangement is postponed pending completion of my studies of the skeletons of several *Telmatobius (sensu lato)*. The separation of *Alsodes* from all other leptodactylids rests on the presence of pectoral plates of nuptial spines. Some species of *Telmatobius* (*jelskii* group) have pectoral plates, as does *Insuetophrynus acarpicus* (Barrio, 1970).

If Fitzinger's (1843) paper antedates Bell's

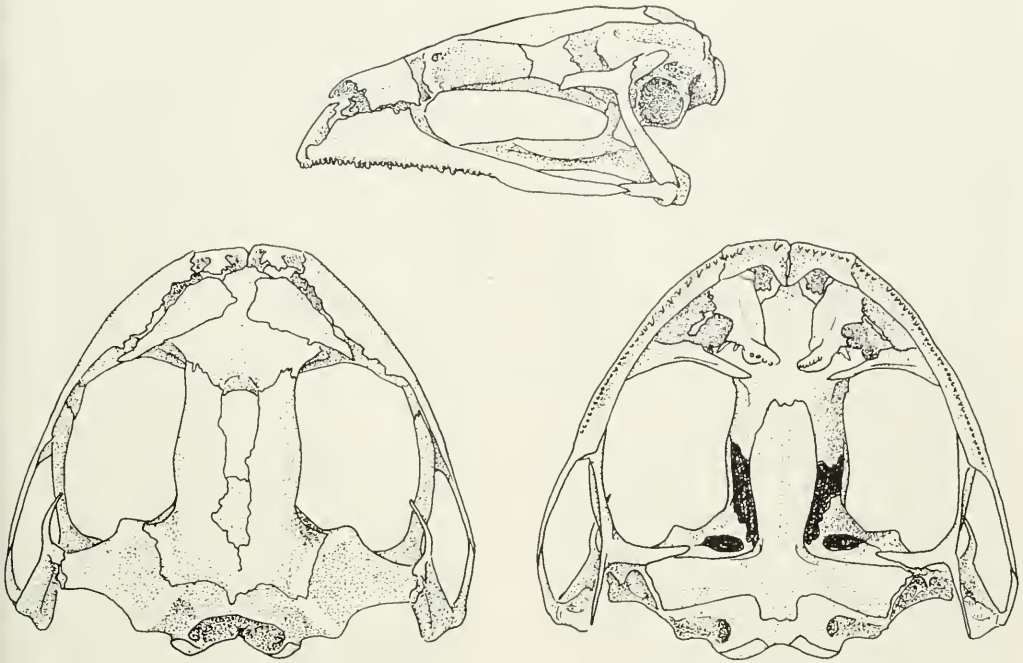

FIGURE 83. Lateral, dorsal, and ventral views of skull of *Eupsophus roseus* (AMNH 22104, × 4.5).

Eusophus Cope, 1865, Rev. Nat. Hist., 5:113 [Emendation (?) of *Eupsophus* Fitzinger, 1843].

Borborocactes Cope, 1866, J. Acad. Nat. Sci. Philadelphia, (2)6:94 [Emendation of *Borborocoetes* Bell, 1843, hence taking same type-species].

Cacotus Günther, 1868, Proc. Zool. Soc. London, 1868:482 [Type-species by monotypy, *Cacotus maculatus* Günther, 1868].

Phrynopus Peters, 1873, Mtber. k. Preuss. Akad. Wiss., Berlin, 1873:416 [Type-species by monotypy, *Phrynopus peruanus* Peters, 1873].

Borborocoetea Strand, 1928, Ark. Naturgesch., 92A:55 [Replacement name for *Borborocoetes* Bell, 1843 (preoccupied), hence taking same type-species].

Diagnostic definition.—4) cervical cotylar arrangement type II; 10) alary processes of premaxillae directed posterodorsally, moderately wide at base; 11) palatal shelf of premaxilla relatively deep, palatal process elongate; 13) palatal shelf of maxilla of moderate width, pterygoid process moderately large; 14) maxillary arch complete, quadratojugal present; 15) nasals small, widely separated medially; 16) nasals in broad contact with maxillae, not in contact with pterygoids; 22) epiotic eminences prominent; 23) cristae paroticae relatively broad, elongate; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal as long as zygomatic ramus, expanded medially into small otic plate; 26) squamosal-maxillary angle 50-55°; 27) columella present or absent; 28) prevomers moderate-sized, separated medially, entire, toothed except in *juninensis*; 29) palatines broad, widely separated medially, bearing odontoid ridges; 30) sphenethmoid entire, extending anteriorly to anterior edge of nasals; 31) anterior ramus of parasphenoid broad, short, keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, broadly overlapped laterally by median rami of ptery-

(1843), as herpetologists have generally presumed, *Hammatodactylus* Fitzinger, 1843 (type-species *Cystignathus nodosus* Duméril and Bibron, 1841) is the correct name for the generic group recognized by Gallardo (1970) and Barrio (1970) and called *Alsodes*.

goids; 33) pterygoids moderate-sized, anterior rami in long contact with maxillae, reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 36) terminal phalanges knobbed; 40) *m. depressor mandibulae* in two slips except in *juninensis* which has only the *pars tympanicus*; 41) pupil horizontal; 42) males with median subgular vocal sac or none; 43) body lacking glands or having extensive, diffuse glandular areas over dorsum; 44) tongue large, round, posterior edge free; 45) toes lacking webbing or fringing to two-thirds webbed; 46) larvae with 2/3 tooth rows, labial papillae interrupted anteriorly; 47) amplexus axillary; 48) eggs small and numerous, laid in gelatinous masses in ponds; 49) males 32-80, females 32-60 mm. SVL; 50) tympanum visible externally, concealed, or absent.

Composition.—Revisionary studies of the Argentine and Chilean species are available (Cei, 1962a, Grandison, 1961, and Gallardo, 1962). As a result of these studies and my own (Lynch, 1971), seven species of the genus are presently recognized: *illotus, juninensis, monticola, nodosus, peruanus, roseus,* and *vertebralis.* The status of the genus in Peru is poorly known.

Distribution.—The Andes of central Peru to Argentina and Chile; between about 10° and 50° S latitude in western South America.

Remarks.—Boulenger (1882) combined a large number of genera and species into *Borborocoetes* Bell (=*Eupsophus*) in his synopsis of living amphibians. While most of his generic groupings were a vast improvement over the previous classifications, *Borborocoetes* was a notable exception. He included a variety of unrelated groups in *Borborocoetes.* The *Borborocoetes* of Boulenger and Noble is best described as a grade (in the sense of Huxley, 1958). All of the species included are members of the Telmatobiinae, and according to the present classification belong to the genera *Batrachyla, Eleutherodactylus, Eupsophus, Ischnocnema, Niceforonia, Thoropa,* and *Zachaenus.*

The Chilean and Argentine species of *Eupsophus* were studied in detail by Cei (1960, 1962a, and 1962b) and Grandison (1961), but they confused one species of *Batrachyla* with *Eupsophus (taeniatus).* Cei (1962a) and Grandison (1961) divided *Eupsophus* into three species groups—*nodosus* group, *peruanus* group, and *roseus* group. These authors also recognized a monotypic *taeniatus* group, which is here included in *Batrachyla.* Two species of the genus (*juninensis* and *monticola* have lost the columella. These species also lack tympanic annuli. The tympanic annulus is very small in two other species of the genus, *illotus* and *nodosus,* and is concealed beneath the skin. In *peruanus, roseus,* and *vertebralis,* the columella is normal-sized and the tympanic annulus is visible externally.

Schaeffer (1949) described, but did not name, a fossil frog from the Lower Oligocene of Chubut, Argentina, and referred it to *Eupsophus.*[11] The nasals of the fossil are apparently in median contact, unlike the condition seen in the living species of the genus. The fossil could equally well be a species of *Telmatobius,* were it not for the fact that the frontoparietal fontanelle is moderately large, not small. The middle ear was not preserved.

Hylorina Bell, 1843
(Fig. 84)

Hylorina Bell, 1843, Zool. Voy. Beagle, Reptiles, 5:44 [Type-species by monotypy, *Hylorina sylvatica* Bell, 1843].

Hylorhina Agassiz, 1846, Nomencl. Zool., index:190 [Emendation of *Hylorina* Bell, 1843, hence taking same type-species].

[11] Bogart (1970) implied that the Oligocene fossil of *Eupsophus* is not separable from living *E. roseus.* However, Schaeffer (1949) cited distinguishing features of the fossil, chiefly in the arrangement of the nasal bones. The Oligocene fossil needs to be restudied to ascertain its distinction from *Telmatobius.*

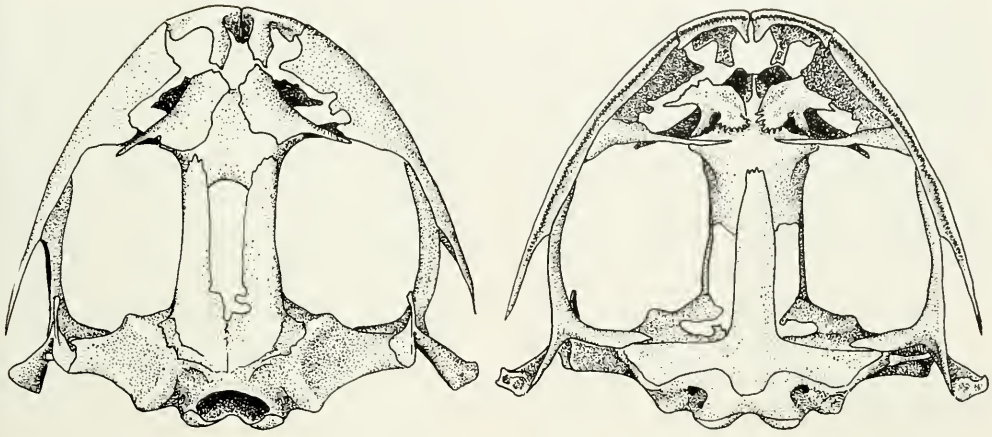

FIGURE 84. Dorsal and ventral views of skull of *Hylorina sylvatica* (BMNH 91.29.17, × 3).

Diagnostic definition.—4) cervical cotylar arrangement type II; 10) alary processes of premaxillae directed dorsally, wide at base; 11) palatal shelf of premaxilla narrow, palatal process relatively small; 13) palatal shelf of maxilla narrow, pterygoid process minute; 14) maxillary arch incomplete, quadratojugal absent, replaced by ligamentous sheath; 15) nasals moderate sized, widely separated medially; 16) nasals in tenuous contact with maxillae, not in contact with pterygoids; 22) epiotic eminences moderately well defined; 23) cristae paroticae short, stocky; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal moderately long, shorter than zygomatic ramus, expanded medially into small otic plate; 26); 27) columella present; 28) prevomers moderately large, entire, narrowly separated medially, toothed; 29) palatines broad, widely separated medially, no odontoid ridges; 30) sphenethmoid entire, extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid broad, short, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids small, anterior rami short, extending to middle of orbit; 34) occipital condyles moderately large, not stalked, narrowly separated medially; 36) terminal phalanges knobbed, elongate; 40) *m. depressor mandibulae* in two slips; 41) pupil vertical; 42) males with median subgular vocal sac; 43) body with glandular dorsolateral folds; 44) tongue large, rounded, posterior edge free; 45) toes lacking webbing or lateral fringes, digital tips narrow, first finger longer than second; 46) larvae with 2/2 tooth rows, labial papillae interrupted anteriorly; 47) amplexus axillary; 48) eggs small, numerous, laid in gelatinous masses at bases of plants in water; 49) males 50-60, females 60-68 mm. SVL; 50) tympanum visible externally; 51) digits extremely long, phalangeal formulae not increased.

Composition.—Monotypic.

Distribution.—Central Chile.

Remarks.—Because *Hylorina* is uncommon, the genus was studied with the aid of stereo-radiographs. *Hylorina* has been considered generically distinct since Bell's description of the type-species. In part the distinction stemmed from erroneous data provided by Boulenger (1882), who reported the sternum as bony. The genus *Hylorina* is very distinctive even though the sternum is a cartilaginous plate which tends to calcify in old adults. The combination of vertical pupil, free toes, greatly elongated digits, externally visible tympanum, and teeth on maxillary arch and prevomerine

dentigerous processes immediately distinguishes *Hylorina* from all other frog genera. In spite of the distinctiveness of *Hylorina*, its skeletal morphology allies it with *Eupsophus*. The data on breeding biology reported by Barrio (1967b) provide additional distinction for *Hylorina*, but also point out the similarity between *Eupsophus* and *Hylorina*.

Batrachyla Bell, 1843
(Fig. 85)

Batrachyla Bell, 1843, Zool. Voy. Beagle, Reptiles, 5:43 [Type-species by monotypy, *Batrachyla leptopus* Bell, 1843].

Diagnostic definition.—4) cervical cotylar arrangement type I; 10) alary processes of premaxillae directed dorsally and somewhat laterally, moderately wide at base; 11) palatal shelf of premaxilla very narrow, palatal process relatively large; 13) palatal shelf of maxilla narrow, pterygoid process lacking; 14) maxillary arch incomplete, quadratojugal absent; 15) nasals widely separated medially, relatively small; 16) nasals separated from maxillae and pterygoids; 22) epiotic eminences obsolete; 23) cristae paroticae stocky, relatively long; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal elongate, widely separated from maxilla; 25) otic ramus of squamosal moderately long, expanding medially into small otic plate; 26) squamosal-maxillary angle about 60°; 27) columella present; 28) prevomers relatively small, entire, separated medially, toothed; 29) palatines curved, narrow, widely separated medially; 30) sphenethmoid entire, extending anteriorly to a point anterior to nasals; 31) anterior ramus of parasphenoid broad, short, lacking median keel; 32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, not overlapped by median rami of pterygoids; 33) pterygoids small, thin, anterior rami short, not extending beyond middle of orbits; 34) occipital condyles small, not stalked, widely separated medially; 36) terminal phalanges T-shaped; 40) *m. depressor mandibulae*

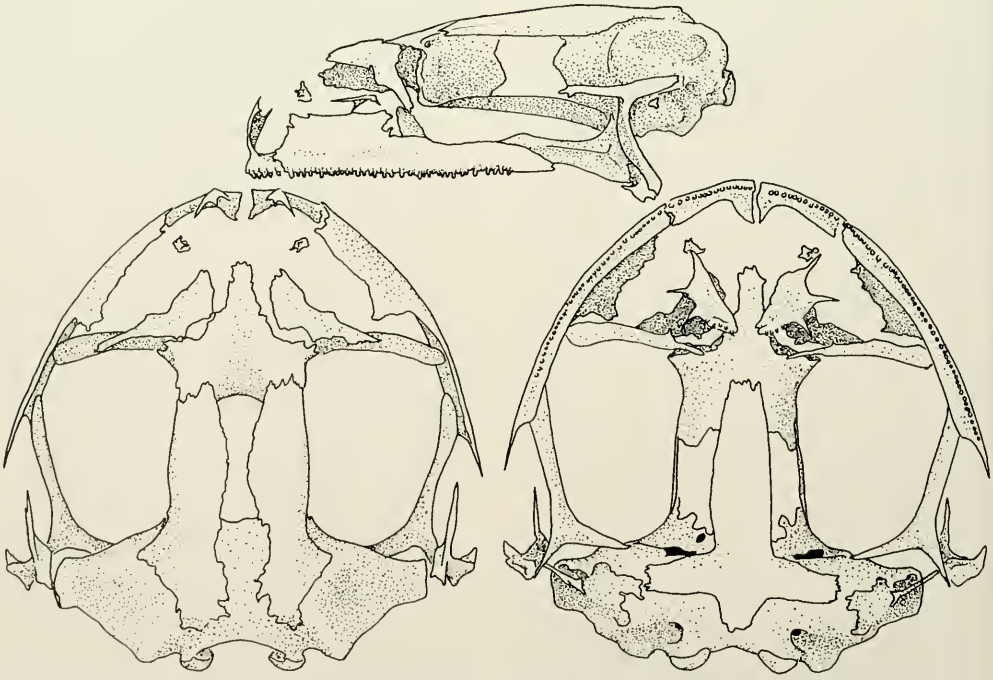

Figure 85. Lateral, dorsal, and ventral views of skull of *Batrachyla leptopus* (UMMZ S-2246, × 6).

in two slips; 41) pupil horizontal; 42) males with median subgular vocal sac; 43) body lacking glands; 44) tongue moderately large, posterior one-third free; 45) toes lacking web or lateral fringes, digital tips bulbous, somewhat dilated, first finger shorter than second; 46) larvae with 2/3 tooth rows, labial papillae not interrupted about mouth; 47) amplexus inguinal; 48) eggs relatively few, large, laid in terrestrial situations, tadpoles become aquatic after nest is inundated; 49) adults 27-40 mm. SVL; 50) tympanum visible externally.

Composition.—Barrio (1967a) recognized two species *(antartandica* and *leptopus)* of *Batrachyla.* Lynch (1971) demonstrated that *Eupsophus taeniatus* belongs to the genus *Batrachyla.*

Distribution.—Chile and adjacent Argentina between 32° and 50° S latitude.

Remarks.—Boulenger (1882) and Myers (1962) considered *Batrachyla* synonymous with *Eleutherodactylus* (*Hylodes* Fitzinger, 1843, in the case of Boulenger). Both authors were under the mistaken impression that the two genera did not differ in significant characters. The two differ as follows (the condition in *Eleutherodactylus* is enclosed in parentheses): quadratojugal absent (present), frontoparietal fontanelle present (absent), nasals small and widely separated medially (large and in median contact), sacral diapophyses dilated (rounded), males with nuptial asperities on thumb (lacking nuptial asperities), aquatic tadpoles (development direct—no tadpole stage), and amplexus inguinal (axillary). The breeding biology of *Batrachyla* is decidedly more primitive than that of *Eleutherodactylus* but approaches the condition of the latter in that the eggs are relatively large, few in number, and laid in moist terrestrial situations (Barrio, 1967a, and Cei, 1962a). In contrast to the eleutherodactyline pattern, tadpoles emerge when the egg hatches and development proceeds in the typical anuran manner.

Thoropa Cope, 1865

(Fig. 86)

Thoropa Cope, 1865, Rev. Nat. Hist., 5:110 [Type-species by monotypy, *Cystignathus missiessii* Eydoux and Souleyet, 1842].

Ololygon Fitzinger (1843) is often cited as an older generic name for *Thoropa.* The type-species of *Ololygon* is *Hyla strigilata* Spix, 1824 (by original designation of Fitzinger, 1843). Therefore, *Ololygon* Fitzinger is a synonym of *Hyla* Laurenti, 1768.

Diagnostic definition.—4) cervical cotylar arrangement type I; 10) alary processes of premaxillae directed dorsally and slightly anteriorly, relatively narrow at base; 11) palatal shelf of premaxilla very narrow with elongate palatal process; 13) palatal shelf of maxilla broad, pterygoid process present; 14) maxillary arch complete, quadratojugal present; 15) nasals relatively large with moderately long maxillary processes, separated medially; 16) nasals not in contact with maxillae or pterygoids; 22) epiotic eminences relatively well defined; 23) cristae paroticae long and narrow in *miliaris,* short and relatively stocky in *lutzi* and *petropolitanus*; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal relatively short; 25) otic ramus of squamosal moderately long, no otic plate; 26) squamosal-maxillary angle 50-70°; 27) columella present; 28) prevomers relatively small, entire, separated medially, toothed; 29) palatines long and narrow, expanded laterally, separated medially; 30) sphenethmoid entire, extending anteriorly to posterior edge of nasals or not reaching nasals; 31) anterior ramus of parasphenoid broad, keeled medially, extending anteriorly to prevomers; 32) parasphenoid alae oriented at right angles to anterior ramus of parasphenoid, relatively short, not overlapped laterally by median rami of pterygoids; 33) pterygoids large, anterior rami in long contact with maxillae, not reaching palatines; 34) occipital condyles large in *miliaris,* small in *lutzi* and *petropoli-*

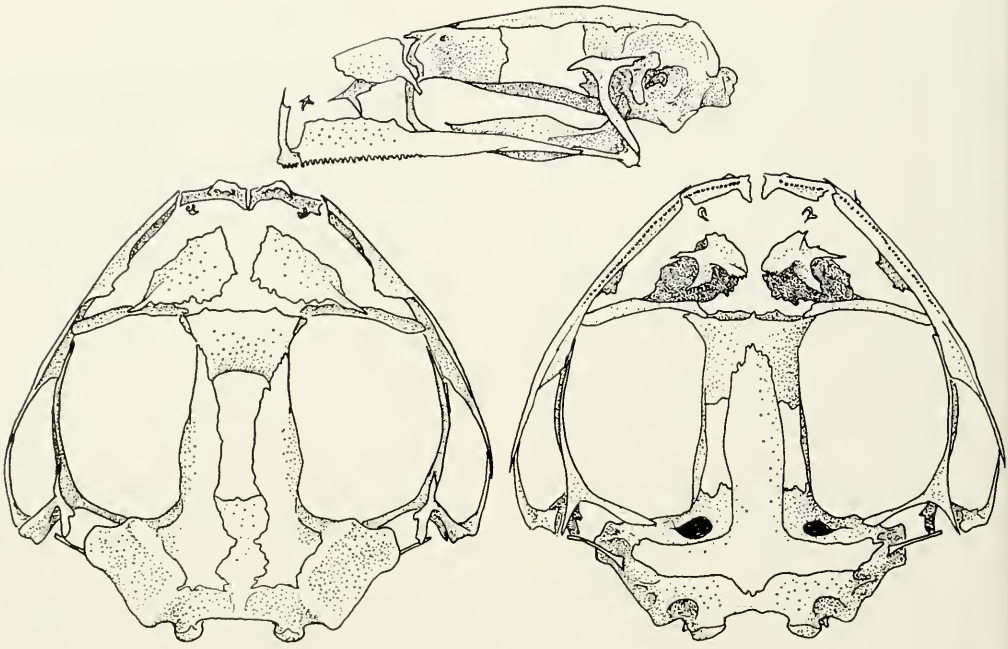

FIGURE 86. Lateral, dorsal, and ventral views of skull of *Thoropa lutzi* (KU 92850, × 4.5).

tanus, not stalked, moderately to widely separated medially; 36) terminal phalanges T-shaped; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median subgular vocal sac; 43) body lacking glands; 44) tongue large, oval, posterior edge free; 45) toes lacking webbing, bearing lateral fringes, digital tips bulbous, somewhat dilated, first finger shorter than second; 46) larvae with 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 47); 48) eggs large, few in number, laid in lotic situations; 49) males 19-78, females 24-70 mm. SVL; 50) tympanum visible externally; 51) tadpoles with greatly flattened and attenuate bodies and tails.

Composition.—Three species were recognized in the revision by Bokermann (1965): *lutzi*, *miliaris*, and *petropolitanus*.

Distribution.—Mountains of southeastern Brasil between 12° and 30° S latitude.

Remarks.—*Thoropa* is least different from *Batrachyla*, although most authors have considered it inseparable from *Eupsophus*. Gallardo (1965) and Lynch (1971) demonstrated the distinctiveness of these two genera. Lutz (1954) suggested that *Thoropa* was closely related to *Cycloramphus*. *Thoropa* and *Cycloramphus* belong to different tribes; this distinction is supported by osteological, non-osteological, and behavioral and larvae data.

Odontophrynini New Tribe

Two genera are included in this tribe —*Odontophrynus* and *Proceratophrys* (the nominal genus *Macrogenioglottus* is inseparable from *Odontophrynus*). *Proceratophrys* is the generic name used herein for the group previously called *Stombus*. The members of this tribe bear considerable external resemblance to the Ceratophryinae, especially *Ceratophrys*. The ilia of the Odontophrynini (Fig. 38) are nearly identical to those of the Ceratophryinae, but the two groups differ in many ways (see subfamily characters for Ceratophryinae and Telmatobiinae). The Odontophrynini are distributed in non-forested and some for-

ested habitats in Argentina, Paraguay, Uruguay, and along the eastern edge of Brasil to Estado de Ceará. Like the other primitive Telmatobiinae, the Odontophrynini have an aquatic stage in the life history, and amplexus is axillary. The following diagnostic characteristics are the same in both genera: 3) transverse processes of posterior presacral vertebrae short; 5) cervical and second vertebrae free; 6) cranial bones not involved in dermostosis; 7) omosternum lacking; 9) maxillary arch toothed, teeth blunt, pedicellate; 11) palatal shelf of premaxilla broad, weakly notched, palatal process large; 12) facial lobe of maxilla deep; 14) maxillary arch complete; 16) nasals in contact with maxillae and pterygoids; 18) frontoparietal fontanelle lacking; 20) frontoparietals not fused with proötics; 21) temporal arcade lacking; 22) epiotic eminences prominent; 23) cristae paroticae long and narrow; carotid artery passes dorsal to skull bones; 27) columella present; 28) prevomers relatively small, entire, toothed, narrowly separated medially; 29) palatines large, narrowly separated medially, bearing odontoid ridge, expanded laterally; 30) sphenethmoid large, entire, extending anteriorly to front edge of nasals; 31) anterior ramus of parasphenoid narrow, pointed, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids large, anterior rami long, in broad sutural contact with maxillae, maxillary process of nasals, and palatines; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 42) males with median, subgular vocal sac; 44) tongue large, round, posterior edge free; 46) larvae with median vent, 2/3 tooth rows, and labial papillae broadly interrupted anteriorly; 47) amplexus axillary; 48) eggs small, numerous, laid in gelatinous masses in ponds; 50) tympanum concealed.

The pectoral girdle is not as massive as in the Telmatobiini, and the omosternum has been lost in the Odontophrynini. The occipital condyles are more widely separated in *Odontophrynus* than in *Proceratophrys* (Figs. 87-88). The cervical cotylar pattern of both genera is type II, although the cotyles are more widely spaced in *Odontophrynus* (Fig. 79). In several character complexes, the Odontophrynini are intermediate between the Ceratophryinae and the Telmatobiini, but they also bear some resemblance to the Eleutherodactylini.

Odontophrynus Reinhardt and Lütken, 1862

(Fig. 87)

Odontophrynus Reinhardt and Lütken, 1862, Vid. Meddel. Naturh. Foren., 13:159 [Type-species by monotypy, *Odontophrynus cultripes* Reinhardt and Lütken, 1862].

Hyperoodon Philippi, 1902, Supl. Bat. Chilenas, p. 1 [Type-species by monotypy, *Hyperoodon asper* Philippi, 1902; preoccupied by *Hyperoodon* Lacépéde, 1804 (Mammalia: Cetacea)].

Macrogenioglottus Carvalho, 1946, Bol. Mus. Rio de Janeiro, (new ser.) 73:1 [Type-species by original designation, *Macrogenioglottus alipioi* Carvalho, 1946].

Diagnostic definition.—4) cervical cotylar arrangement type II, but cotyles well separated medially; 8) sacral diapophyses slightly dilated; 10) alary processes of premaxillae directed posterodorsally, long, relatively narrow at base; 13) palatal shelf of maxilla broad, pterygoid process small or lacking; 14) maxillae not expanded posteriorly; 15) nasals relatively large, keeled, narrowly separated anteriorly; 17) nasals not in contact with frontoparietals; 19) frontoparietals not ornamented except for ridge around posterior half of the braincase roof; 24) zygomatic ramus of squamosal long, tapering, widely separated from maxilla; 25) otic ramus of squamosal long, expanded medially into narrow otic plate; 26) squamosal-maxillary angle 50-55°; 34) occipital condyles

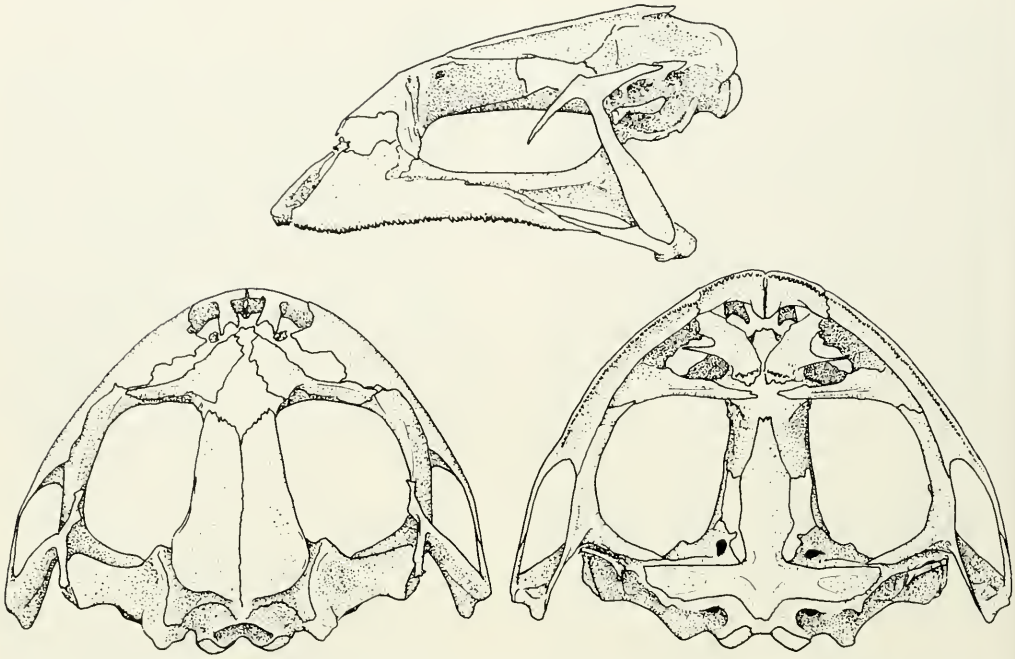

FIGURE 87. Lateral, dorsal, and ventral views of skull of *Odontophrynus carvalhoi* (KU 100441, × 3.2).

large, not stalked, median separation moderate; 42) males with nuptial asperities on thumb; 43) parotoid and/or temporal or tibial glands present; 45) toes about one-half webbed, outer metatarsal tubercle present, inner metatarsal tubercle enlarged and spade-like, digital tips narrow, relatively few supernumerary tubercles on plantar surfaces, first finger longer than second; 49) males 30-60, females 34-70 mm. SVL.

Composition.—Savage and Cei (1965) recognized four species *(americanus, carvalhoi, cultripes,* and *occidentalis).* The type species of *Macrogenioglottus, Odontophrynus alipioi* (Carvalho) [new combination] is here added to the genus.

Distribution.—Semi-arid and arid non-forested habitats of northern Argentina, southern Bolivia and Paraguay, Uruguay, and along the coastal provinces of southeastern and eastern Brasil to Bahía.

Remarks.—Carvalho (1946) named *Macrogenioglottus alipioi* on the basis of two specimens from Bahía, Brasil. The genus was distinguished from all others on the basis of the greatly enlarged *m. genioglottus,* slightly dilated sacral diapophyses, short coccyx, and slightly different positions of the prevomerine dentigerous processes. The myological distinction between *Macrogenioglottus* and *Odontophrynus* remains valid, but with the description of *O. carvalhoi* (Savage and Cei, 1965), the other differences between the two genera were mitigated. The architecture of the temporal region of *alipioi* was figured by Limeses (1965) and is like that of other species of *Odontophrynus.* Savage and Cei (1965) recognized two groups in *Odontophrynus,* one for *cultripes* and *occidentalis,* and another for *americanus* and *carvalhoi. Odontophrynus alipioi* belongs to the latter group and seems closely related to *carvalhoi.* The two species share many characteristics but differ (insofar as is known at present) in some body proportions, color pattern, and colors in life. *Odontophrynus alipioi* has been collected recently near São Paulo (W. C. A. Bokermann, pers. comm.).

Boulenger (1882) confused *Odonto-*

phrynus with *Ceratophrys, Lepidobatrachus,* and *Proceratophrys.* The ceratophryine leptodactylids are readily separated from the two telmatobiine genera in that the derm of the head is fused with the skull bones and a dermostosed vertebral shield is present in the Ceratophryinae. In addition, the Ceratophryinae have non-pedicellate teeth whereas all other leptodactylids (if dentate) have pedicellate teeth. *Odontophrynus* and *Proceratophrys,* especially those of the *bigibbosa* group, are somewhat difficult to separate on external characters alone. The thenar surfaces of *Proceratophrys* are covered with numerous conical supernumerary tubercles, whereas the thenar surfaces of *Odontophrynus* lack supernumerary tubercles or have relatively few, non-conical supernumerary tubercles. Some, but not all, species of *Odontophrynus* have body glands (parotoid, temporal, or tibial), whereas no species of *Proceratophrys* has glands. Osteologically, the two genera are readily separated. *Proceratophrys* has a complete post-orbital bridge (squamosal only), and *Odontophrynus* has a "normal" squamosal. *Proceratophrys* has extensive exostosis of the frontoparietal bones and *Odontophrynus* has no exostosis of the frontoparietals but does have a ridge around the posterior half of the frontoparietal shelf.

Philippi (1902) named *Hyperoodon asper* on the basis of two specimens from Montevideo, Uruguay. Subsequent authors credited him with naming *Hyperoodon* as a new genus although Philippi obviously credited the genus to Duméril and Bibron. *Hyperoodon* Philippi is probably a misspelling for *Uperodon* Duméril and Bibron, a microhylid genus. Nieden (1923) tentatively referred *Hyperoodon asper* to *Paludicola*; the nominal species is currently considered a possible synonym of *Physalaemus gracilis* (Gorham, 1966).

Cei (1958) correctly pointed out that *Hyperoodon asper* is an *Odontophrynus* and tentatively suggested that *asper* was identical with *O. americanus.* Inexplicably, Savage and Cei (1965) did not consider the nominal species in their review of *Odontophrynus.* There is no question, in view of Philippi's description and Cei's (1958) publication of Philippi's long-lost plates, that *Hyperoodon asper* is an *Odontophrynus,* except for Philippi's remarks that maxillary and premaxillary teeth are lacking in the types. Philippi further recorded the presence of prevomerine teeth, suggesting that his observation on the lack of maxillary and premaxillary teeth was erroneous. *Hyperoodon asper* cannot be considered a synonym of any species of *Physalaemus*; it is here transferred to the synonymy of *Odontophrynus americanus.*

Proceratophrys Miranda-Ribeiro, 1920
(Fig. 88)

Proceratophrys Miranda-Ribeiro, 1920, Rev. Mus. Paulista 12:301 [Type-species by monotypy, *Ceratophrys bigibbosa* Peters, 1872].

Diagnostic definition.—4) cervical cotylar arrangement type II, cotyles closely approximated; 8) sacral diapophyses rounded; 10) alary processes of premaxillae long, strongly directed posterodorsally, except in *bigibbosa* group, relatively narrow at base; 13) palatal shelf of maxilla broad, pterygoid process prominent; 14) maxillae slightly expanded posteriorly; 15) nasals relatively narrow, keeled, separated medially (*boiei* group) or in contact (*bigibbosa* group) medially; 17) nasals in contact with frontoparietals; 19) frontoparietals bear lateral crests which meet posteriorly; frontoparietal crests heavily exostosed posteriorly in *cristiceps* and probably in *bigibbosa*; 24) zygomatic ramus of squamosal broad and elongate, in sutural contact with maxilla, weakly exostosed; 25) otic ramus of squamosal large, exostosed, expanded medially into relatively large otic plate; 26) squamosal-maxillary angle 40-50°; 34) occipital condyles large, not stalked, closely juxtaposed;

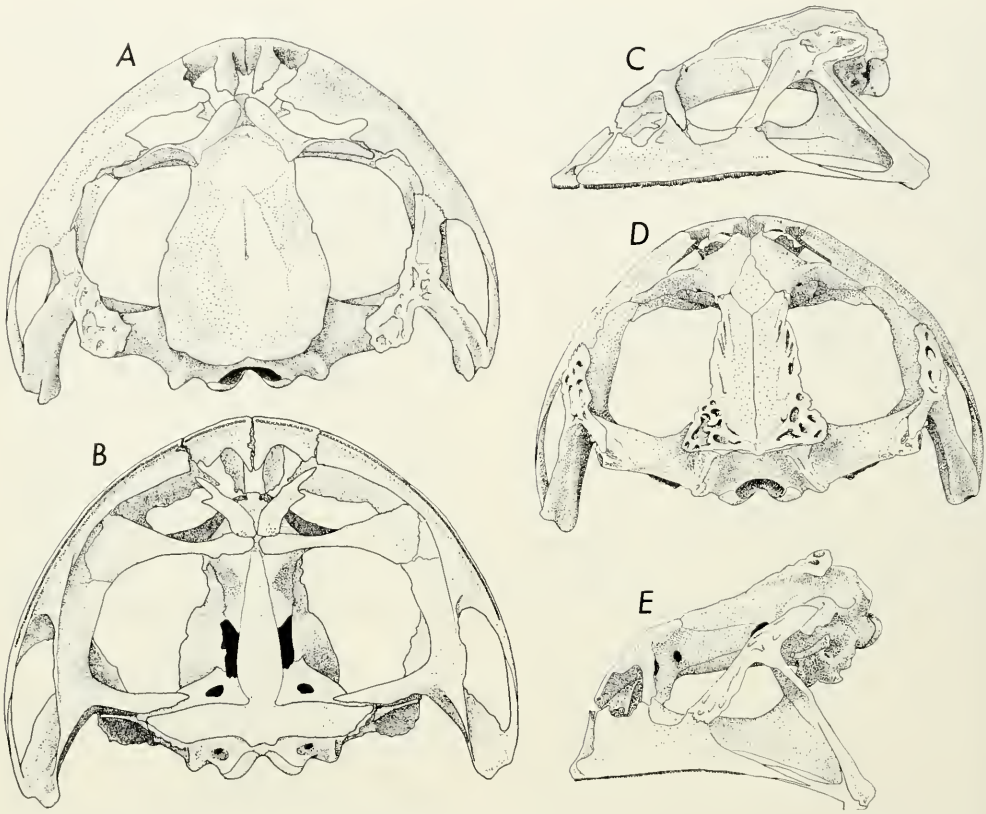

FIGURE 88. (A-C) Dorsal, ventral and lateral views of skull of *Proceratophrys boiei* (KU 93076) and (D-E) dorsal and lateral views of skull of *P. cristiceps* (KU 106273). All × 2.2.

42) males lacking nuptial asperities on thumb; 43) body lacking glands; 45) toes free of webbing, usually with lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle small or enlarged and spade-like, digital tips narrow, numerous conical supernumerary thenar and plantar tubercles, first finger longer than second; 49) adults 30-95 mm. SVL.

Composition.—Eight of the nominal species listed as *Ceratophrys* by Gorham (1966) belong to this genus: *appendiculata, bigibbosa, boiei, cristiceps, fryi, goyanus, renalis,* and *schirchi.* Gorham (1966) did not list *Stombus melanopogon* Miranda-Ribeiro, 1926. Bokermann (1966) considered *boiei, melanopogon, renalis,* and *schirchi* synonymous and used *boiei,* the oldest name. He also considered *goyanus* a synonym of *cristiceps.*

Distribution.—The lowland zone east of the Brasilian Highlands from Fortaleza (Ceará) to Santa Catarina, Brasil, and adjacent Misiones Province, Argentina.

Remarks.—Almost all of the literature pertaining to species of this genus has accumulated under the generic name *Stombus,* a synonym of *Ceratophrys* (see pp. 107-10). Reig and his students have consistently argued that *Stombus (auctorum)* is generically distinct, but they have also repeatedly questioned the generic position of *cristiceps.* I include *cristiceps* in the genus *Proceratophrys* and consider *bigibbosa* its closest relative; this arrangement is similar to that used by Reig in that *cristiceps* is not considered especially closely related to *appendiculata, boiei,* and *fryi.* The differences between *bigibbosa* and *cristiceps* on the one hand, and *appendiculata,*

boiei, and *fryi* on the other, are not of the magnitude I would use at the generic level. The five species form a group on the basis of the thenar and plantar tubercle arrangement, body shape, and the architecture of the temporal region. The two species groups differ in head shape and the correlated and underlying cranial architecture (snout is elongate and sloping in *boiei* group, blunt and short in *bigibbosa* group) and in the development of cranial exostosis (Fig. 88). The differences in musculature that Limeses (1964, 1965) cited as suggestive of separate genera are trivial differences; greater ranges of variation occur within *Odontophrynus* and several other frog genera. The species of the *bigibbosa* group are less unlike *Odontophrynus* in external features than are the species of the *boiei* group. In the *boiei* group, the eyelids are provided with elongate "horns," whereas in the *bigibbosa* group, the eyelid has only a few large tubercles.

Grypiscini Mivart, 1869

Grypiscina Mivart, 1869:295.
Cyclorhamphinae Lutz, 1954:175.
Cycloramphiinae: Gallardo, 1965:84.

Three genera are included in this tribe—*Crossodactylodes, Cycloramphus,* and *Zachaenus.* The nominal genus *Craspedoglossa* is here considered to be a synonym of *Zachaenus.* The tribe name is based on *Grypiscus* Cope, a synonym of *Cycloramphus* Tschudi. At first glance, this group seems to be highly heterogeneous, especially when one considers the supposed relationships of the leptodactylid genera as recognized by herpetologists in the 1910-1930 period when the following genera (all of this group) were recognized: *Craspedoglossa, Cycloramphus, Grypiscus, Iliodiscus, Oocormus,* and *Zachaenus.* Miranda-Ribeiro (1926), Lutz (1954), and Cochran (1955) considered *Zachaenus* to be closely related to *Ceratophrys. Oocormus* was often recognized even by Lutz after she pointed out that it was a synonym of *Zachaenus* (1944). Various authors including Noble (1931) suggested that *Cycloramphus* was closely related to *Telmatobius. Cycloramphus, Iliodiscus,* and *Grypiscus* were usually considered valid until Bokermann (1951) pointed out that they were not generically distinct. Lutz (1954) included only *Cyclorhamphus (sic)* and *Thoropa* in the subfamily, Lutz and Carvalho (1958) considered *Paratelmatobius* to be a generic link between *Cycloramphus* and *Batrachophrynus* and *Telmatobius,* and Gallardo (1965) placed *Craspedoglossus (sic), Cycloramphus, Holoaden,* and *Zachaenus* in the subfamily Cycloramphiinae. All of these authors used labile characters (head shape and toe webbing) to define their groupings. Most of the genera that have been considered related to *Cycloramphus* are burrowing frogs and have long, flat snouts.

The following diagnostic characteristics are the same in the included genera: 3) transverse processes of posterior presacral vertebrae not shortened; 4) cervical cotylar arrangement type I; 5) cervical and second vertebrae free; 6) cranial bones not involved in dermostosis; 9) maxillary arch toothed, teeth blunt, pedicellate; 12) facial lobe of maxilla deep, not exostosed; 14) maxillary arch complete, maxilla expanded posteriorly, quadratojugal deep; 15) nasals relatively large, in broad median contact; 17) nasals in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 20) frontoparietal not fused to proötic; 21) temporal arcade lacking; 23) cristae paroticae very short, stocky; carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal attenuate, curved, widely separated from maxilla; 25) otic ramus of squamosal long, curved medially and expanded medially to form otic plate which rests on crista parotica; 34) occipital condyles relatively small, not stalked, widely separated medially; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in

two slips; 41) pupil horizontal; 47) amplexus axillary.

The developmental pattern of *Cycloramphus* and *Zachaenus* is intermediate between the typical pattern of an aquatic tadpole and the eleutherodactyline pattern of direct development (Lutz, 1944). The eggs are deposited in terrestrial situations (usually in very wet leaves on the forest floor) and the tadpole hatches and lives in the moist, decomposing gelatinous mass. The tadpoles can survive in an aquatic medium but do not feed (Lutz, 1944). *Crossodactylodes* lays only a few large eggs in bromeliads and the tadpole develops in the moist axillae of the bromeliads (W. C. A. Bokermann, pers. comm.).

Holoaden, *Paratelmatobius*, and *Thoropa* do not agree with the diagnostic characteristics listed above and are included in other groups; *Holoaden* is in the Eleutherodactylini, *Paratelmatobius* in the Leptodactylinae, and *Thoropa* in the Alsodini.

The three genera of the tribe occur in forested montane areas in southeastern Brasil and Uruguay. Two of the species presently placed in *Zachaenus* (*roseus* and *sawayae*) are not members of that genus. Their status is discussed in the account of *Zachaenus*.

Crossodactylodes Cochran, 1938
(Fig. 89)

Crossodactylodes Cochran, 1938, Proc. Biol. Soc. Washington, 51:41 [Type-species by original designation, *Crossodactylodes pintoi* Cochran, 1938].

Diagnostic definition.—7) omosternum relatively small; 8) sacral diapophyses dilated; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla relatively broad, broadest laterally, with long palatal process; 13) palatal shelf of maxilla broad anteriorly, narrow over most of its length, pterygoid process lacking; 16) nasals in tenuous contact with maxillae, not in contact with pterygoids; 17) nasals in tenuous contact with frontoparietals, narrowly separated from frontoparietals; 19) frontoparietals not ornamented, lacking sagittal crest; 22) epiotic eminences obsolete; 26) squamosal-maxillary angle

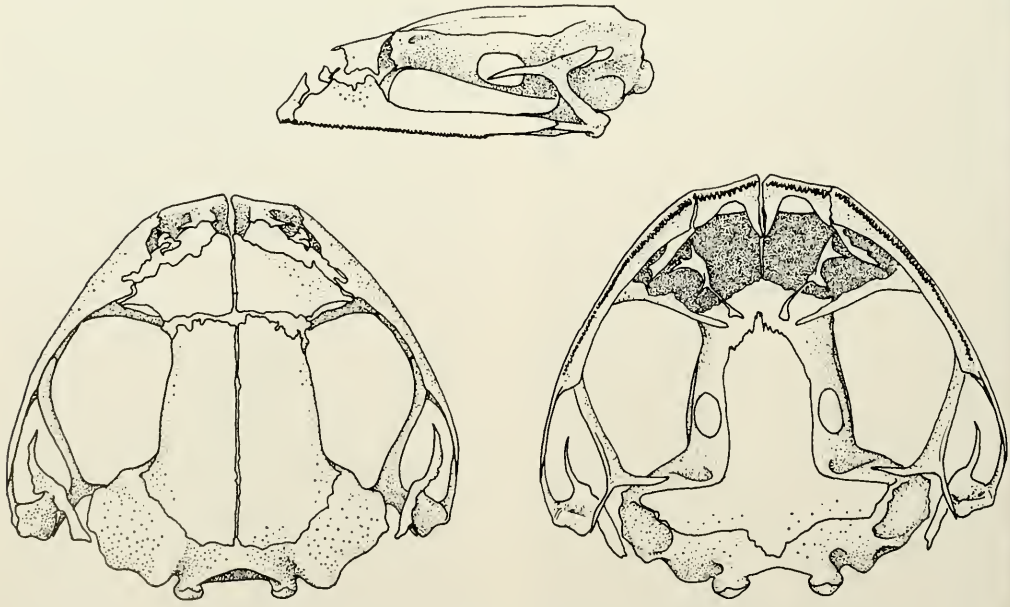

FIGURE 89. Lateral, dorsal, and ventral views of skull of *Crossodactylodes pintoi* (paratype, USNM 120611, × 8).

about 45°; 27) columella absent; 28) prevomers small, edentate, dentigerous rami almost completely lost, widely separated medially; 29) palatines narrow, widely separated medially, lacking odontoid ridges; 30) sphenethmoid entire, extending anteriorly beneath nasals; 31) anterior ramus of parasphenoid broad, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively small, anterior rami extending to middle of orbit, ventral pterygoid flange small; 36) terminal phalanges Y-shaped, lateral processes long and slender; 37-39); 42) males with median subgular vocal sac; males with cluster of spines on thumb; 43) body lacking glands; 44) tongue oval, posterior one-third free, non-boletoid; 45) toes not webbed, lacking lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged and spade-like, digital tips enlarged into pads, first finger shorter than second; 46) tadpoles semi-aquatic; 48) eggs large, few in number, deposited in terrestrial bromeliads; 49) males 15-17.5 mm. SVL; 50) tympanum absent (not hidden, as stated by Cochran, 1938, 1955).

Composition.—Monotypic.

Distribution.—The Coastal Ranges of Guanabara and Espiríto Santo, Brasil.

Remarks.—Cochran (1938, 1955) considered *Crossodactylodes* to be related to *Crossodactylus* (Elosiinae). She based her opinion on the presence of a cluster of spines on the thumbs of the males of both genera and the erroneous opinion that both genera have dermal glands on the top of each digital pad. Cochran noted that when the digital tips of *Crossodactylodes* were dried out, a weak furrow appeared in the center of the digital pad; she considered this condition a precursor of the condition seen in elosiines (distinct dermal glandular pads). The apparent glands observed by Cochran are an artifact resulting from the presence of Y-shaped terminal phalanges. Cochran pointed out that the two genera shared the loss of prevomerine teeth; the prevomerine bones are much smaller in *Crossodactylodes* than in *Crossodactylus,* which usually has larger prevomerine dentigerous processes and rarely prevomerine teeth.

The architecture of the temporal region and the size of the roofing bones of *Crossodactylodes* are like the condition seen in *Cycloramphus* and *Zachaenus.* The other cranial characters of *Crossodactylodes* are not contrary to the conditions which obtain in *Cycloramphus* and *Zachaenus,* although *Crossodactylodes* is separable from these two genera by many skull characters. The data on breeding biology were provided by Werner Bokermann *(in litt.)* and suggest that *Crossodactylodes* is more closely related to *Cycloramphus* and *Zachaenus* than to the Eleutherodactylini, which it resembles in many osteological features.

Cycloramphus Tschudi, 1838

(Fig. 90)

Cycloramphus Tschudi, 1838, Classif. Batr., p. 81 [Type-species by monotypy, *Cycloramphus fulginosus* Tschudi, 1838].

Cyclorhamphus Agassiz, 1846, Nomencl. Zool., index, p. 110 [Emendation of *Cycloramphus* Tschudi, 1838, hence taking same type-species].

Pithecopsis Günther, 1859, Cat. Bat. Sal. British Mus., p. 22 [Type-species by monotypy, *Pithecopsis fuliginosus* (Tschudi, 1838)].

Grypiscus Cope, 1867, J. Acad. Nat. Sci. Philadelphia, (2)6:206 [Type-species by monotypy, *Grypiscus umbrinus* Cope, 1867].

Iliodiscus Miranda-Ribeiro, 1920, Rev. Mus. Paulista, 12:267 [Type-species by subsequent designation (Bokermann, 1951), *Telmatobius brasiliensis* Steindachner, 1864; his designation is hereby rejected (see "Remarks") and the type-species is here designated as *Iliodiscus dubius* Miranda-Ribeiro, 1920].

Niedenia Ahl, 1923, Zool. Anz., 58:107 [Type-species by monotypy, *Niedenia spinulifer* Ahl, 1923].

Diagnostic definition.—7) omosternum moderate-sized; 8) sacral diapophyses rounded to very slightly dilated; 10) alary processes of premaxillae

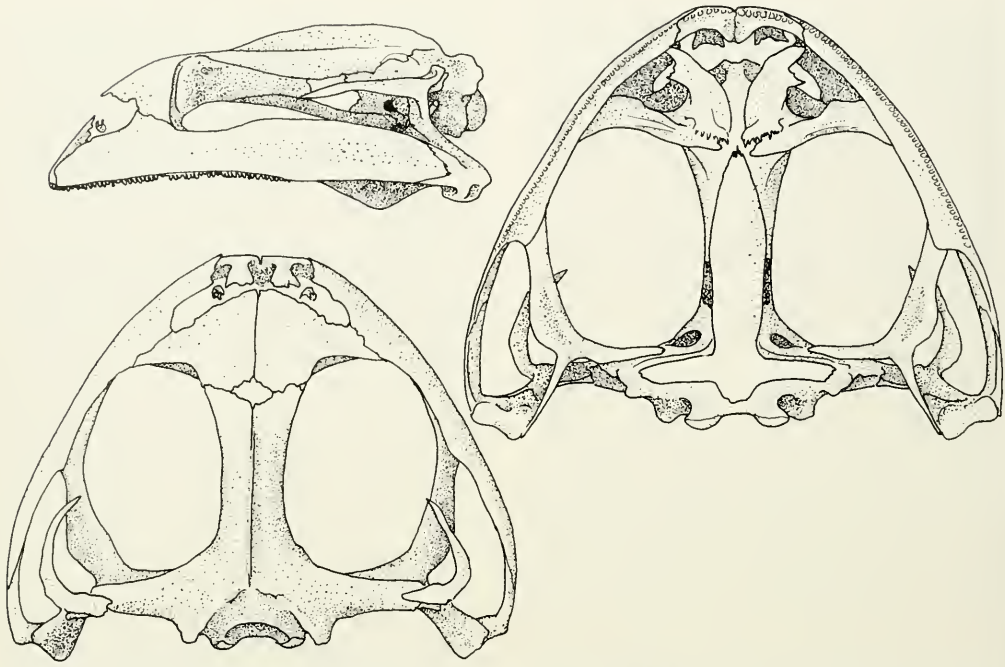

FIGURE 90. Lateral, dorsal, and ventral views of skull of *Cycloramphus eleutherodactylus* (KU 92785, × 3.6).

directed posterodorsally, relatively broad at base; 11) palatal shelf of premaxilla of moderate depth, not notched, palatal process short; 13) palatal shelf of maxilla relatively narrow, pterygoid process large; 16) nasals in contact with maxillae, not with pterygoids; 19) frontoparietals not ornamented, bearing large sagittal crest; 22) epiotic eminences prominent posteriorly, obsolete anteriorly; 26) squamosal-maxillary angle less than 43°, measurement difficult because of curvature of both elements; 27) columella present; 28) prevomers present, entire, moderately large, toothed, separated medially; 29) palatines broad, widely separated medially, bearing small odontoid ridges; 30) sphenethmoid entire, extending anteriorly beneath nasals, not visible dorsally or only a small area visible between junctions of nasals and frontoparietals; 31) anterior ramus of parasphenoid broad, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped by median rami of pterygoids; 33) pterygoids relatively small, anterior rami extending to middle of orbit, pterygoids bearing large ventral flange—cf. Fig. 25; 36) terminal phalanges knobbed; 42) males with median subgular vocal sac; males lacking nuptial asperities except for *C. ohausi* which has a cluster of spines on each thumb; 43) inguinal glands present; 44) tongue large, round, semi-boletoid; 45) toes free of webbing, bearing lateral fringes, or partly to fully webbed, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged and spade-like, digital tips narrow, first finger not longer than second; 46) larvae with very brief tadpole stage, semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly; 48) eggs laid in moist terrestrial situations, hatch near end of larval period, eggs large, few in number (Lutz, 1929); 49) adults 30-55 mm. SVL; 50) tympanum concealed.

Composition.—Seven to nine species are recognized depending on the author. Gorham (1966) listed eight species—

asper, diringshoefensi, eleutherodactylus, fulginosus, granulosus, neglectus, ohausi, and *umbrinus,* whereas Bokermann (1966) recognized *boulengeri, dubius,* and *pinderi* as valid (which Gorham considered synonyms of other names) and placed *umbrinus* in the synonymy of *fulginosus.* The most recent revision of the genus is that of Bokermann (1951), although Cochran (1955) studied a large part of the genus. In view of the differences of opinion as to how many, and which, species are valid, a thorough generic review is desirable.

Distribution.—Forested habitats in southeastern Brasil.

Remarks.—Within comparatively recent times (Miranda-Ribeiro, 1926, Noble, 1931), the genus *Cycloramphus* was divided into three genera *(Cycloramphus, Grypiscus,* and *Iliodiscus).* Bokermann (1951) and Cochran (1955) combined the three into a single genus. Cochran (1955) suggested that the genus is heterogeneous because *C. ohausi* mitigates some of the differences between *Ceratophrys, Cycloramphus,* and *Crossodactylus.* Her statements reflect a philosophy of single-character classification and do not accurately indicate the homogeneity of the genus *Cycloramphus.*

The generic partitioning of *Cycloramphus* was based on the variation in webbing of the toes and Cope's argument that the presence of pseudoteeth on the lower jaw of *umbrinus* justified generic distinction. I have not observed odontoids on the lower jaw of any species of the genus, although Noble (1922) figured a serrate lower jaw of a cotype of *umbrinus.* Six species of the genus *(asper, diringshoefensi, dubius, eleutherodactylus, granulosus,* and *pinderi)* lack webbing or lateral fringes on the toes; three species *(boulengeri, fulginosus,* and *neglectus)* have one-half to fully webbed toes. The two groups are bridged by *ohausi* which has basal webbing and lateral fringes on the toes. The basal webbing probably is best regarded as the broadened junction of the fringes. I consider the lack of webbing to be primitive, because the allied *Zachaenus* lacks webbing.

Bokermann (1951) designated *Telmatobius brasiliensis* Steindachner *(=Cycloramphus fulginosus)* as the type-species of *Iliodiscus* Miranda-Ribeiro, 1920. This action rendered *Iliodiscus* a strict synonym of *Cycloramphus.* However, Miranda-Ribeiro (1920) placed the webless species of *Cycloramphus* in *Iliodiscus; Telmatobius brasiliensis* was included in *Cycloramphus,* not *Iliodiscus,* and therefore cannot be considered for subsequent designation as the type-species of *Iliodiscus.* Accordingly, Bokermann's (1951) restriction is hereby rejected. Miranda-Ribeiro (1920) included four nominal species in *Iliodiscus (dubius, eleutherodactylus, pinderi,* and *semipalmatus).* Gorham (1966) listed *dubius* as the type-species. I designate *I. dubius* Miranda-Ribeiro, 1920, as the type-species of *Iliodiscus* Miranda-Ribeiro, 1920.

Zachaenus Cope, 1866

(Figs. 91-93)

Zachaenus Cope, 1866, J. Acad. Nat. Sci. Philadelphia, 6:94 [Type-species by original designation, *Cystignathus parvulus* Girard, 1854].

Oocormus Boulenger, 1905, Ann. Mag. Nat. Hist., (7)16:181 [Type-species by monotypy, *Oocormus microps* Boulenger, 1905].

Craspedoglossa L. Müller, 1922, Blatter Aquar. Terr., 33:167 [Type-species by monotypy, *Craspedoglossa sanctaecatharinae* L. Müller, 1922].

Diagnostic definition.—7) omosternum relatively large; 8) sacral diapophyses rounded; 10) alary processes of premaxillae directed sharply posterodorsally, relatively broad at base; 11) palatal shelf of maxilla relatively deep, not notched, palatal process moderate-sized; 13) palatal shelf of maxilla of moderate width, pterygoid process lacking; 16) nasals in contact with maxillae, not with pterygoids; 19) frontoparietals not ornamented except for prominent sagittal crest and supraorbital processes; 22)

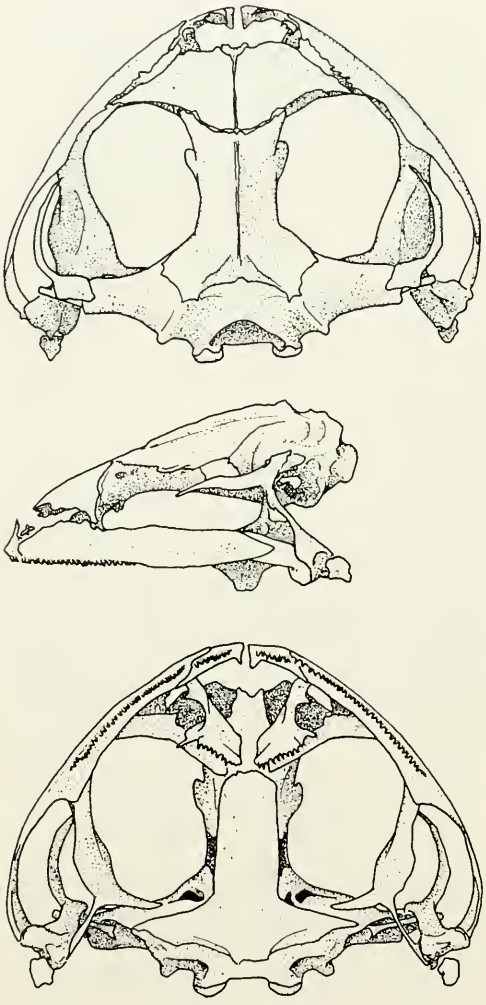

FIGURE 91. Dorsal, lateral, and ventral views of skull of *Zachaenus parvulus* (KU 107090, × 7.5).

epiotic eminences obsolete; 26) squamosal-maxillary angle about 45°; 27) columella present; 28) prevomers relatively large, entire, toothed, narrowly separated medially; 29) palatines slender, widely separated medially, no odontoid ridges; 30) sphenethmoid entire, usually not visible dorsally; 31) anterior ramus of parasphenoid narrow, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively small, anterior rami extending to middle of orbit, large ventral flange; 36) terminal phalanges knobbed; 42) males with median subgular vocal sac; males lacking nuptial asperities; 43) body lacking glands; 44) tongue round, semi-boletoid; 45) toes lacking webbing and lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle enlarged, not spade-like, digital tips narrow, first finger as long as second; 46) development abbreviated, tadpole semi-aquatic, vent median, 1/1 tooth rows, labial papillae broadly interrupted anteriorly (Lutz, 1944); 48) eggs large, few in number, deposited in moist, terrestrial situation, larvae hatch and remain in

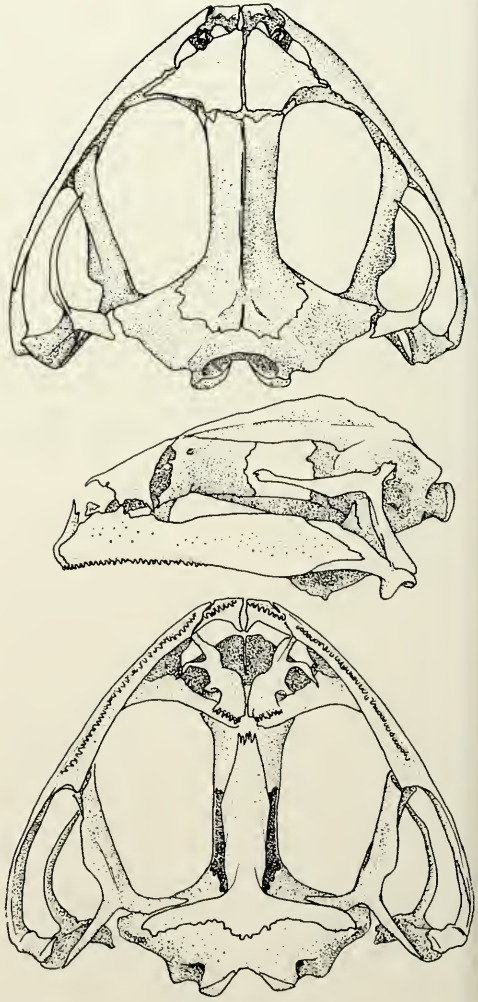

FIGURE 92. Dorsal, lateral, and ventral views of skull of *Zachaenus stejnegeri* (KU 92742, × 7.5).

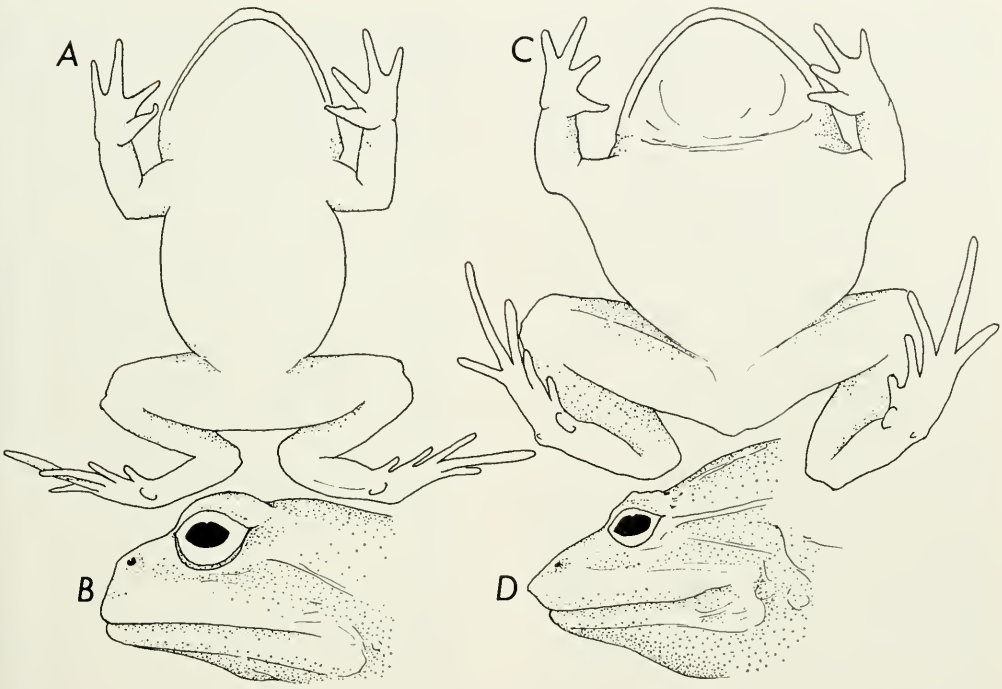

FIGURE 93. Body outlines and sides of heads of (A-B) *Zachaenus stejnegeri* (KU 92744) and (C-D) Z. *parvulus* (KU 93078). All × 2.

gelatinous mass until metamorphosis; 49) adults less than 30 mm. SVL; 50) tympanum concealed.

Composition.—The nominal species of *Craspedoglossa (bolitoglossa, sanctaecatharinae,* and *stejnegeri)* and of *Zachaenus (parvulus, roseus,* and *sawayae).* Bokermann (1966) considered *sanctaecatharinae* to be a synonym of *bolitoglossus.* I do not consider *roseus* or *sawayae* members of this genus (see Remarks).

Distribution.—Southern and southeastern Brasil.

Remarks.—Lutz (1944) demonstrated that *Oocormus microps* is a synonym of *Zachaenus parvulus.* Parker (1926) noted the striking similarities in color pattern and proportions between *Oocormus microps (=Zachaenus parvulus)* and *Sminthillus brasiliensis (=Euparkerella),* which occur sympatrically in southeastern Brasil. Boulenger (1905) confused them and included *Euparkerella* in the syntypic series of *Oocormus microps* as juvenile specimens. The two genera belong to different tribes and can be distinguished externally only by the shape and lengths of the fingers and toes (Fig. 94).

Craspedoglossa is here placed in the synonymy of *Zachaenus* for the first time. Cochran (1955) pointed out that the two nominal genera might be best combined but separated them on the basis of the axillary patagium of *Zachae-*

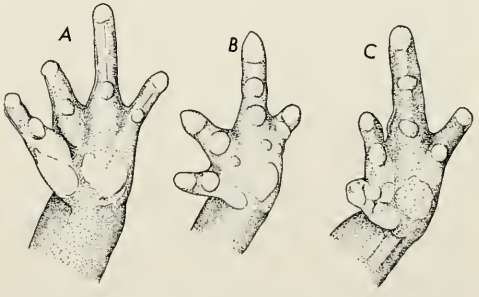

FIGURE 94. Hands of three frogs of the Telmatobiinae. (A) *Zachaenus parvulus* (KU 93078, × 4), (B) *Euparkerella brasiliensis* (KU 112370, × 6.6), and (C) *Scythrophrys sawayae* (USNM 125530, × 6.6).

nus (see Fig. 93). *Telmatobufo* is the only other leptodactylid with an axillary patagium, although the loose, "baggy" skin of *Batrachophrynus* and the strictly aquatic *Telmatobius* produces a poorly defined patagium. The snout is more sloping in *Zachaenus parvulus* than in *Craspedoglossa (sensu strictu).* The axillary patagium is used as a species-group character in other groups of frogs (for example, the *Hyla marmorata* and *H. godmani* groups), and is best regarded as a species-group character here as well. In all other characters used in the generic diagnoses, *Craspedoglossa* and *Zachaenus* are identical.

Cope (1890) named a second species of the genus *(roseus)* based on a single specimen from Port Otway, Patagonia; the unique holotype is now a macerated heap of fragments (Cochran, 1955, 1961b). The original description includes several points that clearly disassociate *roseus* from *Zachaenus* (tympanum visible, tongue not boletoid, prevomerine dentigerous processes small and round, outer metatarsal tubercle lacking, and toes fringed). The osteological data provided by Cope (nasals small, widely separated medially, and frontoparietals complete, i.e., no fontanelle) and those observed by me (pterygoid lacking ventral flange, zygomatic ramus of squamosal short and straight otic ramus of squamosal not curved medially but expanded medially into small otic plate) clearly disassociate *roseus* from *Zachaenus.* Unfortunately, the present data are insufficient for generic assignment. *Zachaenus roseus* Cope is tentatively considered a *species inquirenda* in the family Leptodactylidae, probably in the Telmatobiinae.

Cochran (1953) named a single specimen of a frog from Paraná, Brasil, as a third species of *Zachaenus (sawayae).* The species is clearly not a *Zachaenus,* although its relationships are not apparent; only the holotype is known, and no osteological observations can be made. *Zachaenus sawayae* is considered by me to be the type-species of a new genus of the Telmatobiinae; the tribal relationships are not apparent. The new genus is named at the end of the account of the Telmatobiinae.

Eleutherodactylini Lutz, 1954

Eleutherodactylinae Lutz, 1954:175.

Lutz (1954) proposed this subfamily for the inclusion of *Eleutherodactylus* alone; as was the case with the Cycloramphinae, she did not provide any diagnostic statements for the new group. Gallardo (1965) included *Basanitia, Ctenocranius, Eleutherodactylus, Microbatrachylus,* and *Syrrhophus* in the Eleutherodactylinae. I include the following genera in the tribe Eleutherodactylini: *Amblyphrynus, Eleutherodactylus, Euparkerella, Holoaden, Hylactophryne, Ischnocnema, Niceforonia, Sminthillus, Syrrhophus,* and *Tomodactylus.* The nominal genera *Basanitia, Noblella, Phrynanodus,* and *Trachyphrynus* are considered to be synonyms of *Eleutherodactylus* (Lynch, 1968c, 1968d). The nominal genera *Noblella* Barbour and *Pseudohyla* Andersson are considered to be synonyms of *Eleutherodactylus* (see below).

The following diagnostic characteristics are the same in all of the included genera: 3) tranverse processes of posterior presacral vertebrae not shortened; 4) cervical cotylar arrangement type I; 5) cervical and second vertebrae not fused; 8) sacral diapophyses rounded; 9) maxillary arch usually toothed, if toothed, teeth blunt, pedicellate; 14) maxillary arch complete, maxillae tapering posteriorly, quadratojugal shallow; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle usually absent; 21) temporal arcade lacking; 23) carotid artery passes dorsal to skull bones; 41) pupil horizontal; 42) males lacking nuptial asperities; 45) outer metatarsal tubercle present, inner metatarsal tubercle not spade-like; 46) development direct in known species; 47) amplexus axillary in known species; 48)

eggs relatively large, few in number, deposited in terrestrial situations, bromeliads, etc., in all known species.

Except for the nature of the T-shaped terminal phalanges, the skeleton of the eleutherodactylines is relatively generalized. The sternum is cartilaginous, an omosternum is usually present and relatively large, the cervical cotyles are widely separated medially, the transverse processes of the presacral vertebrae are neither greatly expanded nor shortened, the sacral diapophyses are rounded or only slightly dilated, the ilia are of the leptodactyline type, all cranial bones are present although a few species have lost the prevomerine bones or the columellae. The cranial bones are not dermostosed but exostosis is developed in several groups. The nasals are large and usually in median contact, and the frontoparietal fontanelle is rarely developed. There is considerable variation in the size and shape of the zygomatic ramus of the squamosal among the genera and species of this tribe, and most of the variation is observed within *Eleutherodactylus.*

Morphologically, the tribe Eleutherodactylini is difficult to define. The relationships of ten genera I include in this tribe are not entirely obvious. The definition of the group rests solely on the mode of reproduction, and the included genera are judged to be related because the various sections of the tribe can be tied together through the use of several different character complexes. Species of the following genera are known to lay terrestrial eggs and to lack a free tadpole stage: *Eleutherodactylus, Holoaden, Hylactophryne, Sminthillus, Syrrhophus,* and *Tomodactylus. Euparkerella* and *Niceforonia* probably lay large terrestrial eggs, judging from the size of mature eggs and the oviducts. Reproductive data are not available for *Amblyphrynus* and *Ischnocnema.* Females of the latter genus have moderately large, unpigmented eggs, but the eggs are not so large as to be suggestive of direct development. However, the eggs of *Ischnocnema* are no smaller than those of *Eleutherodactylus maussi,* which exhibits direct development (Heatwole, 1962). *Eleutherodactylus, Sminthillus, Syrrhophus,* and *Tomodactylus* have broadly T-shaped terminal phalanges. The terminal phalanges of *Euparkerella* are broad and small, but could not be accurately described as T-shaped. The terminal phalanges of the other five genera *(Amblyphrynus, Holoaden, Hylactophryne, Ischnocnema,* and *Niceforonia)* of the tribe are knobbed. *Amblyphrynus* bears considerable resemblance to the *Eleutherodactylus cornutus* group and differs only in the nature of the terminal phalanges. *Hylactophryne* and *Ischnocnema* bear considerable resemblance to one another and to the *Eleutherodactylus binotatus* and *guentheri* groups; these genera also differ only in the nature of the terminal phalanges. *Niceforonia* is superficially similar to *Eupsophus* and to the *Eleutherodactylus unistrigatus* complex (several species groups are involved). *Niceforonia* differs from *Eupsophus* in several osteological characters as well as in reproductive pattern, but differs from the *Eleutherodactylus unistrigatus* complex only in the nature of the terminal phalanges. *Holoaden* is not obviously related to any group of *Eleutherodactylus,* but is osteologically similar to *Niceforonia.*

Amblyphrynus Cochran and Goin, 1961

Amblyphrynus Cochran and Goin, 1961, Fieldiana, Zool., 39:543 [Type-species by original designation, *Amblyphrynus ingeri* Cochran and Goin, 1961].

Diagnostic definition.—7) omosternum present; 9) maxillary arch toothed; 10) alary processes of premaxillae directed posterodorsally; 11); 12) facial lobe of maxilla deep, not exostosed; 13); 15) nasals large, in broad median contact; 16) nasals in tenuous contact with maxillae, not in contact with pterygoids; 19) frontoparietal bears large, well defined, exostosed, lateral crests; 20); 22)

epiotic eminences obsolete; 23) cristae paroticae long, narrow; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal short, not expanded medially into otic plate; 26); 27) columella present; 28) prevomers large, entire, toothed, in median contact; 29) palatines large, narrowly separated medially; 30) sphenethmoid entire, extending anteriorly beneath nasals; 31) anterior ramus of parasphenoid broad, not keeled, pointed anteriorly; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids of moderate size, lacking ventral flange, anterior rami not reaching palatines, median rami long; 34) occipital condyles large, not stalked, widely separated medially; 36) terminal phalanges knobbed; 37-40); 42); 43) body lacking glands; 44) tongue large, round, posterior edge free; 45) toes free of webbing, digital tips narrow; 46-48); 49) the two known specimens are 51.5 and 83.0 mm. SVL; 50) tympanum visible externally.

Composition.—Monotypic.

Distribution.—Known from two localities in the Andes of central Colombia (850-2350 meters). Peracca's (1914) record of an *Eleutherodactylus cornutus* from the highlands in Departamento Antioquia, Colombia, may refer to this species.

Remarks.—Cochran and Goin (1961) suggested that *Amblyphrynus* is a member of the "broad-headed leptodactylid" group which includes the ceratophryine genera, *Proceratophrys*, and *Zachaenus*. They suggested that *Amblyphrynus* was probably most closely related to *Zachaenus*. The resemblance between these two genera is spurious. This association can only be made by comparison of description of characters and will not bear up against specimen comparison or the additional osteological characteristics. The suggestion that this species is allied with the ceratophryine leptodactylids is contradicted by the lack of morphological agreement between the two groups. The ceratophryines have large, casqued skulls with extensive dermostosis and exostosis, a distinctly different type of cervical-occipital articulation, non-pedicellate teeth, expanded transverse processes of the anterior presacral vertebrae and shortened transverse processes of the posterior presacral vertebrae, and a dermostosed vertebral shield.

In many respects, *Amblyphrynus* resembles the large-headed frogs of the *Eleutherodactylus cornutus* group. The holotype of *Amblyphrynus ingeri* was first reported by Dunn (1944) as an *Eleutherodactylus cornutus*. The only characteristic separating these two groups is the nature of the terminal phalanges. When additional specimens of *A. ingeri* become available an effort must be made to determine if the terminal phalanges of the hind feet are knobbed or T-shaped. As pointed out previously, the terminal phalanges of the fingers may be knobbed and those of the toes T-shaped. This pattern is observed in several groups of *Eleutherodactylus*.

The only specimens of this species available were studied through the use of stereo-radiographs.

Eleutherodactylus Duméril and Bibron, 1841

(Figs. 95-99)

Cornufer Tschudi, 1838, Classif. Batr., p. 28 [Type-species by monotypy, *Cornufer unicolor* Tschudi, 1838 (=*Eleutherodactylus inoptatus*). Suppression of Tschudi's names was requested by Zweifel (1966)].

Eleutherodactylus Duméril and Bibron, 1841, Erp. gén., 8:620 [Type-species by monotypy, *Hylodes martinicensis* Tschudi, 1838. Myers (1962) listed the type-species designation as by original designation. The name *Eleutherodactylus* was included in the synonymy of *Hylodes martinicensis* by Duméril and Bibron (1841). Apparently they had planned to use the generic name in their *Erpetologie généralé* until Tschudi (1838) named their *martinicensis* in the genus *Hylodes*].

Hylodes Fitzinger (*non Hylodes* Fitzinger, 1826), 1843, Syst. Rep., p. 31 [Type-species

by original designation, *Hylodes martinicensis* Tschudi, 1838].

Euhyas Fitzinger, 1843, *Ibid.*, p. 31 [Type-species by original designation, *Hylodes ricordii* Duméril and Bibron, 1841].

Craugastor Cope, 1862, Proc. Acad. Nat. Sci. Philadelphia, p. 153 [Type-species by subsequent designation (Dunn and Dunn, 1940), *Hylodes fitzingeri* O. Schmidt, 1858].

Strabomantis W. Peters, 1863, Mtber. k. Preuss. Akad. Wiss., Berlin, p. 405 [Type-species by monotypy, *Strabomantis biporcatus* W. Peters, 1863].

Leiyla Keferstein, 1868, Ark. Naturges., 34:296 [Type-species by monotypy, *Leiyla guentherii* Keferstein, 1868].

Liyla Cope, 1870, Proc. Amer. Philos. Soc., 11: 160 [Emendation of *Leiyla* Keferstein, 1868].

Limnophys Jiménez de la Espada, 1870, J. Sci. Math., Phys. Nat. Lisboa, 3:59 [Type-species by subsequent designation (Myers, 1962), *Limnophys cornutus* Jiménez de la Espada, 1870].

Pristimantis Jiménez de la Espada, 1870, *Ibid.*, 3:61 [Type-species by monotypy, *Pristimantis galdi* Jiménez de la Espada, 1870].

Cyclocephalus Jiménez de la Espada, 1875, Vert. Viaje Pacif., Batr., pl. 3 [Type-species by monotypy, *Cyclocephalus lacrimosus* Jiménez de la Espada, 1875].

Hypodictyon Cope, 1885, Proc. Amer. Philos. Soc., 22:383 [Type-species by original designation, *Phyllobates ridens* Cope, 1866].

Liohyla Cope, 1894, *Ibid.*, 31:335 [Emendation of *Leiyla* Keferstein, 1868].

Basanitia Miranda-Ribeiro, 1923, Rev. Mus. Paulista, 13:851 [Type-species by monotypy, *Basanitia lactea* Miranda-Ribeiro, 1923].

Noblella Barbour, 1930, Zoologica, 11:81 [Type-species by original designation, *Sminthillus peruvianus* Noble, 1921].

Phrynanodus Ahl, 1933, Zool. Anz., 104:29 [Type-species by monotypy, *Phrynanodus nanus* Ahl, 1933].

Teletrema Miranda-Ribeiro, 1937, O Campo (Rio de Janeiro), 8(89):67 [Type-species by monotypy, *Teletrema heterodactylum* Miranda-Ribeiro, 1937].

Microbatrachylus Taylor, 1940, Univ. Kansas Sci. Bull., 26:499 [Type-species by original designation, *Eleutherodactylus hobartsmithi* Taylor, 1936].

Ctenocranius Melin, 1941, Medd. Göteborgs Mus. Zool. Avd., 88:49 [Type-species by subsequent designation (Myers, 1962), *Limnophys cornutus* Jiménez de la Espada, 1870].

Pseudohyla Andersson, 1945, Ark. Zool., 37A: 86 [Type-species by monotypy, *Pseudohyla nigrogrisea* Andersson, 1945].

Trachyphrynus Goin and Cochran, 1963, Proc. California Acad. Sci., 31:502 [Type-species by original designation, *Trachyphrynus myersi* Goin and Cochran, 1963].

Diagnostic definition.—7) omosternum usually present, small, medium-sized, or large, long and narrow or relatively broad, absent in at least one species—*E. ruthae*; 9) maxillary arch toothed; 10) alary processes of premaxillae relatively broad at base, direction variable—dorsal, dorsolateral, or posterodorsal; 11) palatal shelf of premaxil-

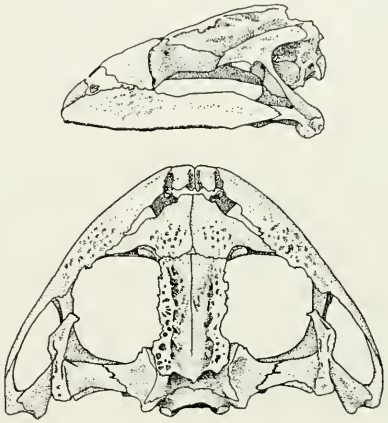

FIGURE 95. Lateral and dorsal views of skull of *Eleutherodactylus sulcatus* (KU 100355, × 2.4).

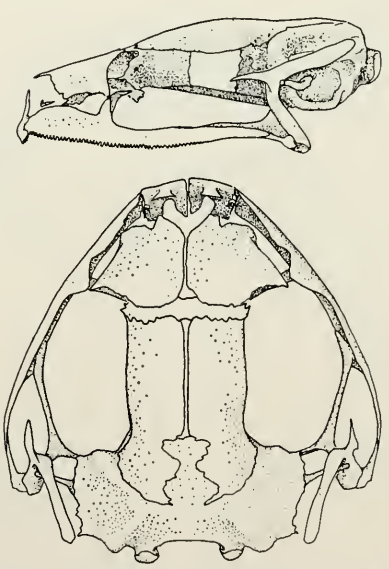

FIGURE 96. Lateral and dorsal views of skull of *Eleutherodactylus diastema* (KU 68263, × 6).

la deep, usually deeply dissected; 12) facial lobe of maxilla deep, usually not exostosed; 13) palatal shelf of maxilla broad, usually with prominent pterygoid process; 15) nasals large, in broad median contact, narrowly separated in some species; 16) nasals not in contact with pterygoids, sometimes in contact with maxillae; 18) frontoparietal fontanelle absent in adults except in *E. palmeri* and *E. whymperi*; 19) frontoparietals not ornamented in most species groups, but bearing lateral crests in *biporcatus, cornutus, galdi,* and *unistrigatus* complexes; 20) frontoparietals fused with proötics or not. The bones are fused in most species in the West Indies and northern Andes, free in other groups; 22) epiotic eminences prominent to obsolete—group variable; 23) cristae paroticae short and stocky to long and narrow; 24) zygomatic ramus of squamosal short to long, sometimes knobbed, in contact with maxilla in one species *(ruthae)*; 25) otic ramus of squamosal short to long, usually forming a small otic plate, ornamented in a few species groups—notably the *galdi* group; 26) squamosal-maxillary angle 44-67°, most 50-60°; 27) columella present; 28) prevomers nearly always toothed, entire, narrowly separated medially to broadly separated medially; 29) palatines long, usually expanded laterally, relatively widely separated medially, no odontoid ridges; 30) sphenethmoid entire, extending anteriorly beneath nasals variable distance; 31) anterior ramus of parasphenoid narrow to broad, relatively long, nearly reaching prevomers, not keeled medially; 32) parasphenoid alae in two patterns: 1. alae deflected posteriorly, short, not overlapped laterally by median rami of pterygoids, and 2. alae oriented at right angles to anterior ramus, rarely deflected posteriorly, long, broadly overlapped by median rami of pterygoids. The first pattern is seen in West Indian species and some Andean species, whereas the second is seen in Central American and lowland South American species; 33) pterygoids slender to relatively massive, lacking ventral flange, anterior rami relatively short, not reaching palatines, median rami short to long, straight or bent; 34) occipital condyles relatively small, stalked or not, widely separated medially; 36) terminal phalanges nearly always clearly T-shaped, inner phalanges usually knobbed, terminal phalanges

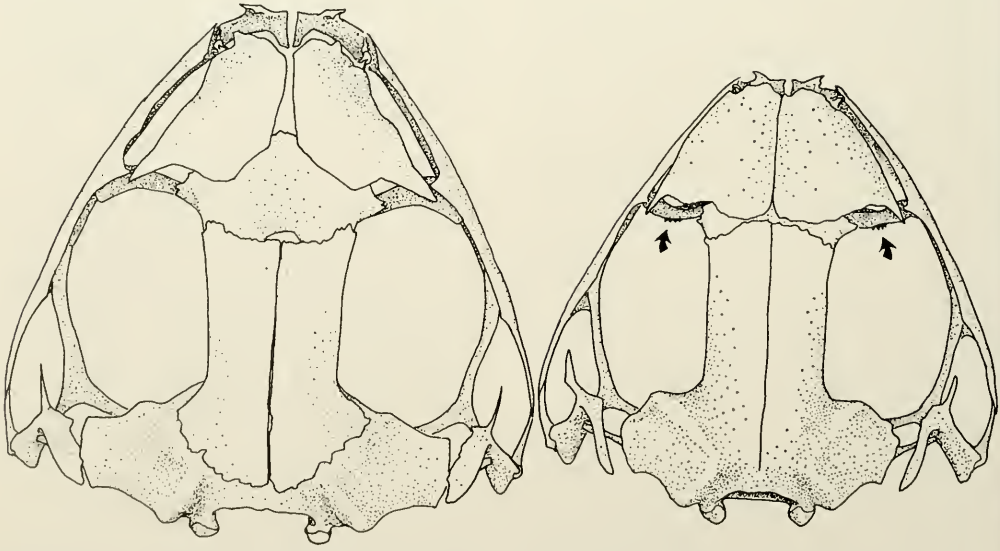

FIGURE 97. Dorsal views of the skulls of *Eleutherodactylus conspicillatus* (KU 108988, × 4.5) and *E. planirostris* (KU 92656, × 4.5). Arrows point to prevomerine teeth which are visible in dorsal view.

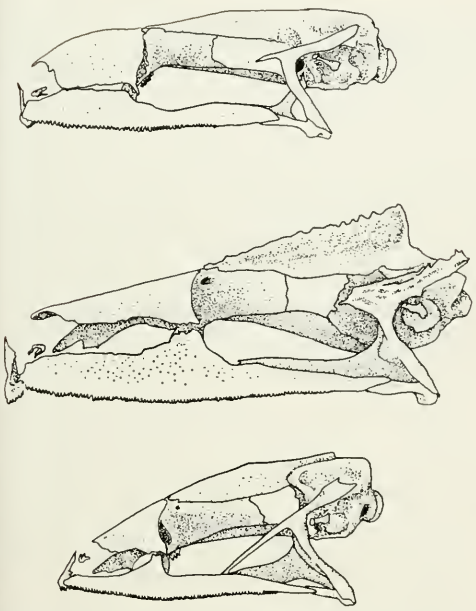

FIGURE 98. Lateral views of skulls of *Eleutherodactylus*. (A) *planirostris* (KU 92656, × 6), (B) *galdi* (USNM field GOV 8944, × 6), and (C) *ruthae* (AS 4237, × 2).

of toes more T-shaped than those of fingers; presence of T-shaped terminal phalanx is expressed externally by the presence of a terminal transverse groove across the tip of the digital pad; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in one slip in *E. galdi*, in one slip with separation into two slips dorsally in species of *biporcatus* and *cornutus* groups, or in two large slips in most species; 42) males with single subgular vocal sac or none, internal or external; 43) glands on body usually absent, those present are usually loosely organized inguinal glands; 44) tongue long and narrow to large and round, posterior edge usually free; 45) toes free of webbing to nearly fully webbed; when webbing is present, it is indicative of a close association with streams, webbing is greatest in *anomalus, karlschmidti, punctariolus,* and *raniformis,* although several species of the *rugulosus* group in Central America have the toes one-half webbed; digits usually bear large pads; 49) adults range from 12-100+ mm. SVL; 50) tympanum absent in *anotis*, concealed in many species, visible externally in most species.

Composition.—Gorham (1966) listed nearly 300 species in the most recent compilation of names in the genus. Albert Schwartz informed me that there are 100 species in the West Indies (including Trinidad). My own estimate is that the genus contains about 400 species, many yet unnamed.

Distribution.—Sinaloa and Tamaulipas, México (but not on the Mexican Plateau) southward and eastward throughout Middle America to northern Argentina and southern Brasil; all West Indian islands; introduced into Florida.

Remarks.—Myers (1962) discussed the generic synonymy of this genus and included most of the generic synonyms listed above as well as *Syrrhophus* and *Lithodytes* in the synonymy of *Eleu-*

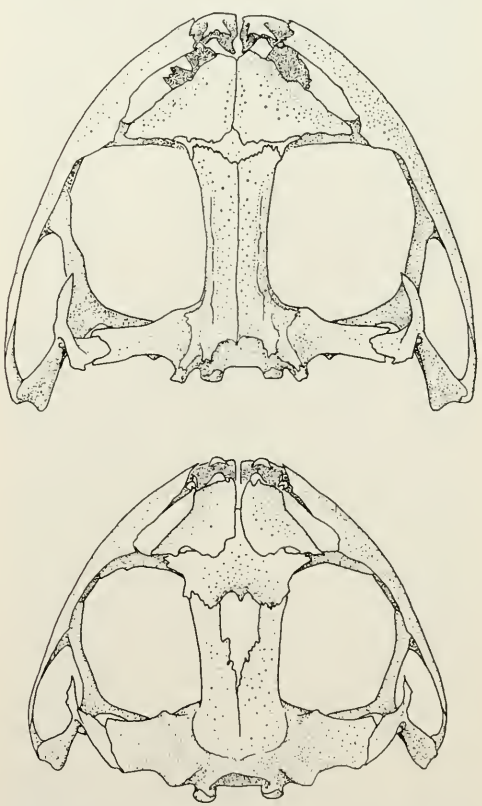

FIGURE 99. Dorsal views of skulls of (top) *Eleutherodactylus bufoniformis* (KU 80621, × 2) and *E. palmeri* (KU 110923, × 3).

therodactylus. Microbatrachylus was synonymized by Lynch (1965), and he later (1968c, 1968d) considered *Basanitia, Phrynanodus,* and *Trachyphrynus* inseparable from *Eleutherodactylus.*

Two generic synonyms are added at this time: *Noblella* Barbour and *Pseudohyla* Andersson. Noble (1921) named *Sminthillus peruvianus* on the basis of several specimens of a minute frog with an anterior epicoracoidal fusion (the distinguishing character of the genus). At the time of the description of *peruvianus,* the genus *Sminthillus* was known only from Cuba, but with the description of a species from southeastern Brasil by Parker (1926), it began to appear that *Sminthillus* was a widespread, Neotropical genus of small frogs. Noble (1926b, 1931) suggested that *Sminthillus* was derived from *Eleutherodactylus* or *Syrrhophus* but placed it in another family (Brachycephalidae). Griffiths (1959) placed each of the three species of *Sminthillus* in a separate genus, utilizing Barbour's (1930) *Noblella* for *peruviana.* Barbour (1930) proposed *Noblella* for *peruviana* because the Cuban species was geographically remote from the two South American species and because he believed *Sminthillus* to be a *Phyllobates* (Dendrobatidae). Griffiths offered a new generic name, *Euparkerella,* for the Brasilian species. *Euparkerella,* while here retained as an eleutherodactyline, is very distinct from all other genera of the tribe and subfamily. *Sminthillus* is retained as a genus of eleutherodactylines on less secure grounds—the maxillary teeth are absent. *Noblella peruviana,* on the other hand, has maxillary teeth, although it apparently has no prevomers. The single specimen of this species available to me cannot be generically separated from *Eleutherodactylus;* an epicoracoidal bridge is not, in my opinion, sufficient basis for the maintenance of an otherwise undefinable generic group (see discussion on page 59). *Noblella* therefore is placed in the synonymy of *Eleutherodactylus.* This action creates one minor problem—Noble's *peruvianus* was proposed in 1921, but Melin (1941) proposed a *Hylodes peruvianus* which becomes a secondary homonym of Noble's name. Rather than propose a replacement name for a probably invalid species, I suggest that Melin's name be kept in mind by the person who eventually studies the *conspicillatus* group in the Amazon Basin of Peru.

Andersson (1945) proposed *Pseudohyla* as a hylid genus, but having studied the holotype of *P. nigrogrisea,* I do not consider the genus separable from *Eleutherodactylus* (Lynch, 1969a). *Eleutherodactylus nigrogriseus* is a small species of the genus and has been found in the valley of the Río Pastaza and on the slopes of the Cordillera Dué in eastern Ecuador.

The genus *Eleutherodactylus* is a large and unwieldy one, although *Hyla* and possibly *Rana* are more unwieldy at present. In contrast to the latter two genera (and perhaps to the opinions of several herpetologists) the genus *Eleutherodactylus* is marked by considerable homogeneity. There is a large range of sizes among the species; most species lack webbing between the toes but some have it, including one species with fully webbed feet *(E. karlschmidti).* Exostosis of the cranial bones is developed in several species groups but in general the phenomenon is an uncommon trait in the genus. Some species have minute digital pads and only small lateral projections of the terminal phalanges on the hands, but all species have moderate to large T-shaped terminal phalanges on the toes (see pp. 65-66 for further discussion).

Three characters exhibit especially interesting variation in *Eleutherodactylus*—1) fusion of the frontoparietal and otoccipital bones; 2) degree of overlap of the parasphenoid alae and median rami of the pterygoids; and 3) median separation of the prevomers. On the basis of the variation in these characters, the species of the West Indies and parts

of the Andean system form one group and the species of México, Central America, and lowland South America form a second group. These characters are discussed below.

Baldauf and Tanzer (1965) improved our knowledge of leptodactylid skulls with the description of the cranium of *Syrrhophus marnockii*. In this work they pointed out the fusion of the frontoparietal and proötic in this species. These bones are fused in all species of *Syrrhophus* and *Tomodactylus*, whereas they are not fused in the *Eleutherodactylus* of México and Middle America. Although fewer than one-third of the species of *Eleutherodactylus* have been studied for this character, I feel that I have checked a sufficiently representative sample in that I have examined species from all parts of the range of the genus. Fusion of the frontoparietal and proötic (otoccipital, since the proötic is usually fused with the exoccipital) occurs in the species of the genus found in the West Indies from Bermuda and the Bahamas (and Florida) to Trinidad. The species of the Hispaniolan *inoptatus* group (*inoptatus* and *ruthae* examined) as well as the Puerto Rican *karlschmidti* apparently have the two bones free. At least some (perhaps all) of the species of the Andean groups exhibit fusion of these bones. No species was examined from the Andes south of Ecuador. All species of the genera *Syrrhophus* and *Tomodactylus* as well as *Sminthillus* exhibit the fusion. No species of *Eleutherodactylus* in México or Central America normally exhibits frontoparietal-proötic fusion (see below), nor do species of the genus found in Chocoan Colombia and Ecuador. Insofar as I am aware, no species found in the Amazon Basin exhibits the fusion nor do the representatives of the genus in southeastern Brasil.

Some variability was noted. One specimen of *E. fitzingeri* (JDL S-407) exhibited fusion of the frontoparietal and otoccipital bones whereas the other nine specimens examined did not. One of three specimens of *E. chloronotus* examined exhibited the fusion. Two of the 19 specimens of *E. curtipes* examined did not exhibit fusion of these bones; both were small specimens, suggesting that the fusion is an ontogenetic phenomenon. In the cases of the first two species, I regard the fusion as aberrant. In each instance, the frontoparietals, nasals, prevomers, and parasphenoid were bound to the sphenethmoid and otoccipitals with no apparent sutures. This suggests that the fusion in these cases resulted from extensive calcification rather than osteological fusion.

The degree of overlap between the median rami of the pterygoids and parasphenoid alae follows the same pattern as the frontoparietal-proötic fusion with some departure. The median pterygoid rami of the *rhodopis* group of *Eleutherodactylus* are short and bent so that there is no actual contact between the pterygoid and parasphenoid, but the median ramus of the pterygoid abuts against the otic capsule just above the parasphenoid ala. In the majority of species of the genus, the median ramus is broadly in contact with the anterior edge of the parasphenoid ala or the median ramus is shortened and may or may not reach the otic capsule and does not reach the shortened parasphenoid ala. In those species with a pterygoid-parasphenoid overlap, the frontoparietals and proötic bones are free. The members of the *rhodopis* complex of *Eleutherodactylus* have the bent pterygoid and hence do not have a typical pterygoid-parasphenoid overlap but because the median rami of the pterygoids are proportionately long, these species are included in the same complex as those species with a broad overlap of the parasphenoid alae and median pterygoid rami. In the *rhodopis* complex the frontoparietal and proötic bones are not fused. Those species with a very short median ramus on the pterygoid and no pterygoid-parasphenoid overlap also exhibit the fused

frontoparietal-proötic. For purposes of further discussion, these two major groups are here termed the Alpha and Beta groups of *Eleutherodactylus*. Members of the Alpha group (fused frontoparietal-proötic, non-overlap between pterygoids and parasphenoid alae) usually have relatively widely separated prevomers, whereas the Beta group frogs (frontoparietal and proötic not fused, pterygoids overlap parasphenoid alae) usually have the prevomers in contact or only narrowly separated.

I submit that the two divisions, Alpha and Beta, are natural divisions within the genus *Eleutherodactylus* and not simply a chaotic array of species exhibiting two osteological patterns. I borrowed the terminology of Etheridge (1960) for the major divisions since at this time I am not willing to afford the two divisions nomenclatorial recognition and prefer the informal divisional names. This course is taken because only a relatively small part of the genus has been surveyed, and many species could not be assigned to subgenus were nomenclatorial assignments made. If the two divisions were accorded nomenclatorial status, the Alpha group would be the subgenus *Eleutherodactylus* and the Beta group would take the name *Craugastor*.

Several osteological features seem to lend themselves well to the possible use of skeletal morphology in the assessment of species group relationships within the genus *Eleutherodactylus*. The degree of median separation of the prevomers has potential in that it varies concordantly with several other osteological traits (the development of cranial crests, shape of the rami of the squamosal, and size and shape of the nasal bones). Among the West Indian species of the genus, the species groups have long been based at least in part on the length of the prevomerine dentigerous processes, and I would expect this character complex to be of at least some value, although its use is greatly hampered by the occasional loss of dentigerous processes in several groups of the genus. I have not attempted to divide the species of the genus into species groups, because I have not studied all species of the genus and I cannot rely upon the literature for many characters that I regard as of potential importance. A study of the osteology of the genus *Eleutherodactylus* is envisioned, but prior to its initiation considerable research must be done in straightening out many nomenclatorial entanglements, the description of many more species, and synonymizing of many names.

Euparkerella Griffiths, 1959
(Fig. 100)

Euparkerella Griffiths, 1959, Proc. Zool. Soc. London, 132:477 [Type-species by original designation, *Sminthillus brasiliensis* Parker, 1926].

Diagnostic definition.—7) omosternum present, small; 9) maxillary arch toothed; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla very broad, not notched, palatal process minute; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla broad, tapering posteriorly, no pterygoid process; 15) nasals small, moderate median separation; 16) nasals in contact with maxillae, separated from pterygoids; 19) frontoparietals not ornamented; 20) frontoparietal fused to proötic; 22) epiotic eminences small; 23) cristae paroticae very broad, stocky; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal elongate, not expanded medially into otic plate; 26) squamosal-maxillary angle about 60°; 27) columella absent; 28) prevomers reduced to minute slivers, widely separated medially, edentate, dentigerous rami lost; 29) palatines very slender, reduced in size, widely separated medially; 30) sphenethmoid divided, extending anteriorly under posterior edge of nasals; 31) anterior ramus of parasphenoid very broad, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior

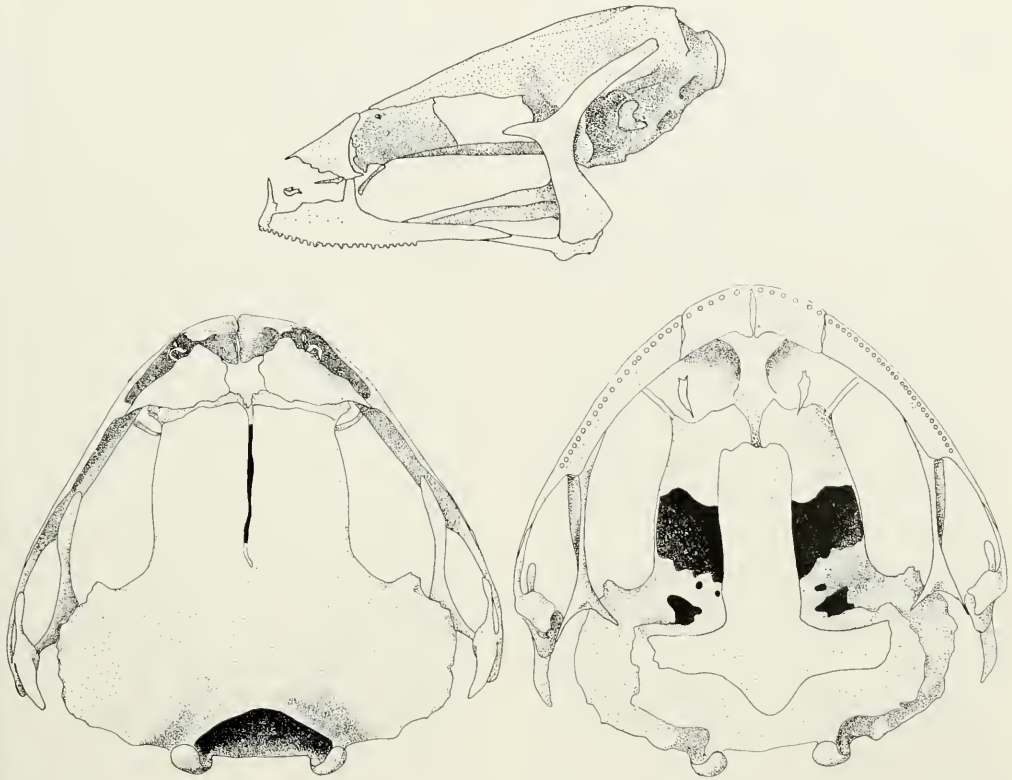

FIGURE 100. Lateral, dorsal, and ventral views of skull of *Euparkerella brasiliensis* (KU 93192, × 5).

ramus, short, not overlapped by median rami of pterygoids; 33) pterygoids relatively small, anterior rami long, not reaching palatines; 34) occipital condyles small, stalked, widely separated medially; 36) terminal phalanges short and broad, bearing small hook-like lateral processes; 37) alary processes lacking on hyoid plate; 40) *m. depressor mandibulae* in two slips; 42) males with median subgular vocal sac; 43) body lacking glands; 44) tongue large, not notched, posterior edge free; 45) toes lacking webbing, digital tips pointed, not dilated, fingers and toes short; 46-48); 49) adults small, less than 20 mm. SVL; 50) tympanum absent.

Composition.—Monotypic.

Distribution.—Known only from the Serra dos Orgãos, state of Guanabara, Brasil.

Remarks.—Parker (1926) named *Sminthillus brasiliensis* on the basis of the "juvenile" cotypes of Boulenger's *Oocormus microps* (=*Zachaenus parvulus*). Noble examined Parker's drawings of the pectoral girdle of *brasiliensis* and agreed with Parker that the species fit the characteristics of *Sminthillus*. At that time, *Sminthillus* comprised three species—one Cuban, one Peruvian, and one Brasilian. Griffiths (1959) argued that if all three species were independent derivatives of *Eleutherodactylus*, then each belongs to a separate genus. His solution was to place each in a monotypic genus. Griffiths proposed *Euparkerella* for the Brasilian species but did not provide diagnostic statements for the genus. *Euparkerella* is very distinctive in its osteology. In external morphology, *Euparkerella* is superficially very similar to *Zachaenus parvulus*. These two species live in the same habitat (leaf litter) in southeastern Brasil and are frequently collected syntopically. The coloration of

the two species is nearly identical. *Euparkerella brasiliensis* and *Zachaenus parvulus* differ in adult size and the length of the fingers (Fig. 94).

The skeleton of *Euparkerella* does not bear any close resemblance to that of any other leptodactylid genus, although the squamosal architecture, lack of columellae, and shape of the hyoid plate of *Euparkerella* suggest a relationship to the genus *Holoaden*. The terminal phalanges of *Euparkerella* are unique in the shape of the lateral expansions (Figs. 43-44). The digits are not pad-like and lack the terminal transverse groove that is found on the digital tips of *Eleutherodactylus, Syrrhophus, Sminthillus,* and *Tomodactylus*. The frontoparietal and proötic fusion of *Euparkerella* is suggestive of a relationship with the Alpha division of *Eleutherodactylus*. At present, I regard the relationships of *Euparkerella* as obscure but feel that the genus is probably more closely related to *Holoaden* than to either division of *Eleutherodactylus*.

Holoaden Miranda-Ribeiro, 1920
(Fig. 101)

Holoaden Miranda-Ribeiro, 1920, Rev. Mus. Paulista, 12:319 [Type-species by monotypy, *Holoaden luederwaldti* Miranda-Ribeiro, 1920].

Diagnostic definition.—7) omosternum moderate-sized; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, moderately wide at base; 11) palatal shelf of premaxilla broad, slightly indented; 12) facial lobe of maxilla relatively shallow, not exostosed; 13) palatal shelf of maxilla of moderate width, no distinct pterygoid process; 15) nasals moderate-sized, narrowly separated medially; 16) nasals separated from maxillae and pterygoids; 18) frontoparietal fontanelle moderate-sized; 19) frontoparietals not ornamented; 20) frontoparietals not fused with proötics; 22) epiotic eminences small; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal moderately long, widely separated from maxilla; 25) otic ramus of squamosal

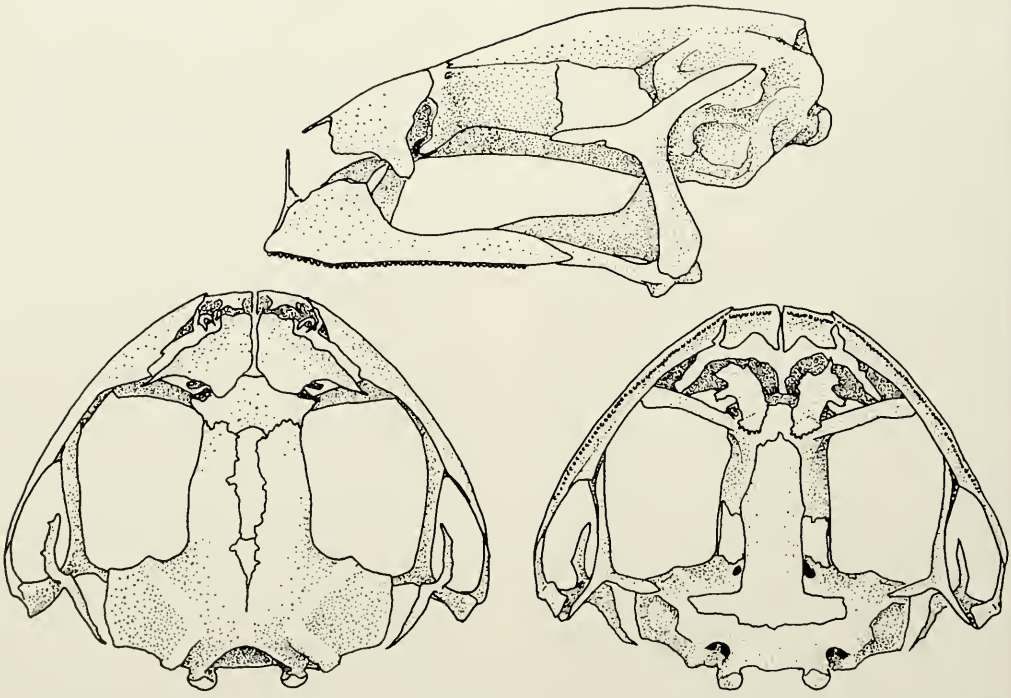

FIGURE 101. Lateral (× 8), dorsal (× 4) and ventral (× 4) views of skull of *Holoaden bradei* (KU 107087).

long, not expanded medially into otic plate; 26) squamosal-maxillary angle about 65°; 27) columella absent; 28) prevomers entire, toothed, separated medially; 29) palatines narrow, elongate, separated medially; 30) sphenethmoid entire, extending anteriorly beneath posterior edge of nasals; 31) anterior ramus of parasphenoid moderately broad, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, widely separated from median rami of pterygoids; 33) pterygoids slender, anterior rami long, nearly reaching palatines; 34) occipital condyles small, not stalked, widely separated medially; 36) terminal phalanges knobbed; 37) hyoid plate lacking alary processes; 40) *m. depressor mandibulae* in two slips; 42) males lacking vocal sac; 43) entire skin glandular forming large, indefinite parotoid, flank, and inguinal glands and a large glandular mass on the thighs; 44) tongue oval, not notched, posterior one-half free; 45) toes free of webbing, digital tips narrow; 49) adults small, 20-48 mm. SVL; 50) tympanum absent.

Composition.—Two species are presently known *(bradei* and *luederwaldti).*

Distribution.—The coastal Serras of southeastern Brasil.

Remarks.—Miranda-Ribeiro (1920, 1926) included *Holoaden* in the Telmatobiidae with *Acris, Iliodiscus,* and *Telmatobius.* He considered the Telmatobiidae to be intermediate between the Hylidae and Leptodactylidae. Lutz (1958) considered *Holoaden* a member of a generic cline *(Cycloramphus-Craspedoglossa-Holoaden)* but did not place the genus in the Cycloramphinae. *Holoaden* is superficially similar to *Zachaenus stejnegeri (Craspedoglossa auctorum)* but differs in several osteological characters. *Holoaden* and *Euparkerella* lack alary processes on the hyoid plate and differ from all other leptodactylids except *Limnomedusa* and *Sminthillus* in this character. *Holoaden* is osteologically similar to the Andean *Niceforonia.* This similarity may reflect a faunal relationship between the Brasilian highlands and the Andes or may reflect convergence in the arrangement of the skull bones resulting from adaptation to burrowing. In osteological and external characters, *Holoaden* does not seem especially closely related to any other genus included in the Eleutherodactylini except *Euparkerella.*

Hylactophryne Lynch, 1968

(Figs. 102-03)

Hylactophryne Lynch, 1968, Univ. Kansas Publs. Mus. Nat. Hist., 17:511 [Type-species by original designation, *Hylodes augusti* Dugés, 1879].

Diagnostic definition.—7) omosternum large; 9) maxillary arch toothed; 10) alary processes of premaxillae directed posterodorsally, moderately wide at base; 11) palatal shelf of premaxilla broad, deeply dissected; 12) facial lobe of maxilla relatively deep, not exostosed; 13) palatal shelf of maxilla of moderate width, pterygoid process large; 15) nasals very large, in broad median contact; 16) nasals in contact with maxillae, not with pterygoids; 19) frontoparietals not ornamented; 20) frontoparietals not fused to proötics; 22) epiotic eminences large; 23) cristae paroticae long, narrow; 24) zygomatic ramus of squamosal of moderate length, not reaching maxilla; 25) otic ramus of squamosal long, as long as zygomatic ramus, expanded medially into small otic plate; 26) squamosal-maxillary angle about 55°; 27) columella present; 28) prevomers large, entire, narrowly separated medially; 29) palatines large, broad, separated medially; 30) sphenethmoid entire, large, extending anteriorly beneath posterior edge of nasals; 31) anterior ramus of parasphenoid broad, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly overlapped by median rami of pterygoids; 33) pterygoids moderate-sized, anterior rami long, reaching palatines; 34) occipital condyles moderate-sized, not stalked, widely separated medially; 36)

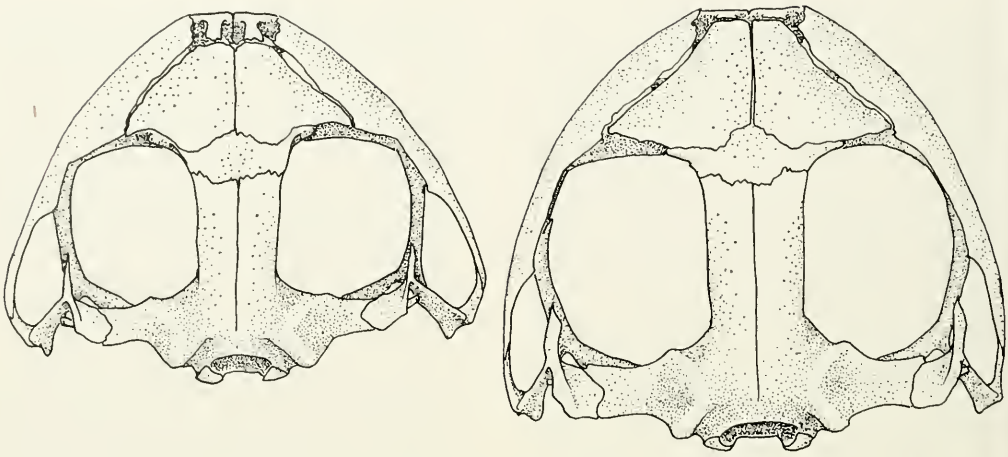

FIGURE 102. Dorsal views of skulls of *Hylactophryne augusti* (KU 56187, × 2.3, left) and *Ischnocnema quixensis* (KU 104388, × 4.7, right).

terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 42) males with median subgular vocal sac; 43) body free of glands; 44) tongue large, oval, posterior edge free; 45) toes free of webbing or lateral fringes, digital tips narrow, first finger longer than second; 49) males 37-77, females 40-95 mm. SVL; 50) tympanum visible externally.

Composition.—Two species are currently recognized *(augusti* and *tarahumaraensis).* The former is composed of four subspecies. The group was revised by Zweifel (1956b).

Distribution.—Mexican Plateau from Arizona, New Mexico, and Texas to cen-

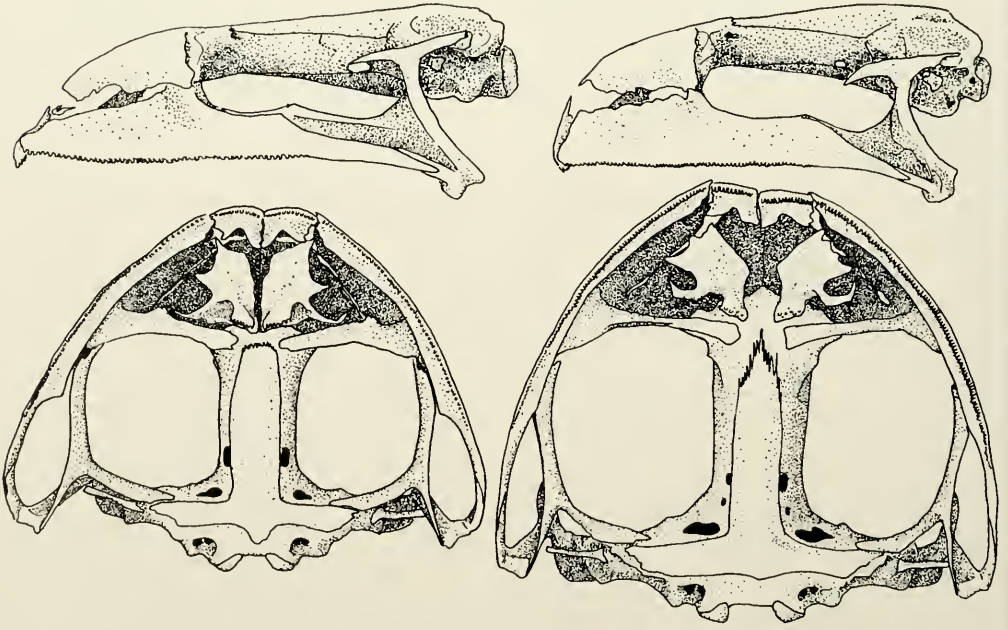

FIGURE 103. Lateral and ventral views of skulls of *Hylactophryne augusti* (KU 56187, × 3, left) and *Ischnocnema quixensis* (KU 104388, × 3 and × 4.7, right).

tral México (Cordillera Volcánica and western Sierra Madre del Sur). An isolated population is known from the mountains in the Isthmus of Tehuantepec.

Remarks.—Hylactophryne is very distinctive when compared with the Central American and Mexican leptodactylids but is less distinctive when compared with some of the South American eleutherodactylines. When I named *Hylactophryne* (Lynch, 1968a), I suggested that the genus was allied to *Eupsophus*. At that time I was under the mistaken impression that *Oreobates quixensis* was an *Eupsophus*. Subsequently, I have examined all of the species of frogs referred to the genus *Eupsophus* by various authors and concluded that the genus *Eupsophus* in the broad sense (that of Noble, 1931, and Gorham, 1966) includes representatives of five genera. One of these genera is *Ischnocnema* (see following account), which contains two species in South America. *Hylactophryne* and *Ischnocnema* are very similar. The skulls of the two genera differ in proportions but are otherwise the same (Figs. 102-03). These genera are tentatively separated on the basis of the presence *(Hylactophryne)* or absence *(Ischnocnema)* of a discoidal fold. The two genera may prove to be independent derivatives of *Eleutherodactylus* rather than primitive as I previously suggested (Lynch, 1968a). The *Eleutherodactylus guentheri* group of frogs bear considerable resemblance to *Ischnocnema quixensis* and *I. verrucosa*. *Eleutherodactylus carrioni* of the southern Ecuadorian Andes is very similar to *Hylactophryne augusti*. In both cases, the species of *Eleutherodactylus* differ from the two genera in having T-shaped terminal phalanges (rather than knobbed phalanges) and in having the terminal transverse groove on the digital pad (rather than no groove or pad). For the present, I do not advocate combining *Hylactophryne* and *Ischnocnema* with one another or with *Eleutherodactylus*.

Ischnocnema Reinhardt and Lütken, 1862

(Figs. 102-03)

Ischnocnema Reinhardt and Lütken, 1862, Vid. Meddel. Naturh., Foren., 1861:239 [Type-species by monotypy, *Leiuperus verrucosus* Reinhardt and Lütken, 1862].

Oreobates Jiménez de la Espada, 1872, An. Soc. Española Hist. Nat., 1:87 [Type-species by monotypy, *Oreobates quixensis* Jiménez de la Espada, 1872].

Diagnostic definition.—7) omosternum moderate-sized; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, moderately wide at base; 11) palatal shelf of premaxilla relatively deep, notched; 12) facial lobe of maxilla deep, not exostosed; 13) palatal shelf of maxilla relatively narrow, pterygoid process large; 15) nasals very large, in broad median contact; 16) nasals separated from maxillae and pterygoids; 19) frontoparietals only slightly ornamented; 20) frontoparietals not fused to proötics; 22) epiotic eminences poorly defined; 23) cristae paroticae relatively long and narrow; 24) zygomatic ramus of squamosal relatively long, widely separated from maxilla; 25) otic ramus of squamosal slightly shorter than zygomatic ramus, expanded medially into small otic plate; 26) squamosal-maxillary angle about 50°; 27) columella present; 28) prevomers large, entire, toothed, narrowly separated medially; 29) palatines large, broad, separated medially, bearing odontoid ridge in *quixensis*; 30) sphenethmoid entire, extending anteriorly beneath posterior edge of nasals; 31) anterior ramus of parasphenoid relatively narrow, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, slightly overlapped laterally by median rami of pterygoids; 33) pterygoids moderate-sized, anterior rami long, reaching palatines; 34) occipital condyles small, on small stalks, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 42) males with median subgular vocal sac;

43) body lacking glands; 44) tongue large, oval, posterior edge free; 45) toes lacking webbing, digital tips narrow, first finger longer than second; 46-48); 49) adults to 55 mm. SVL; 50) tympanum visible externally.

Composition.—Two species are presently known (*quixensis* and *verrucosa*).

Distribution.—Western edge of the Amazon basin in Ecuador, northeastern Peru, and adjacent Brasil *(quixensis)*, and in the coastal Serras of southeastern Brasil *(verruscosa)*. Both species are found in forested habitats.

Remarks.—As mentioned before *(Hylactophryne* account), *Ischnocnema* is very similar to *Hylactophryne*; the two genera are here separated on the basis of trivial external characters, geography, and a lack of knowledge concerning breeding behavior and biology. The similarities in morphology between these two geographically isolated groups of eleutherodactyline frogs is suggestive of an independent origin of each from an *Eleutherodactylus* stock through a departure from the arboreal adaptive zone. Typical *Eleutherodactylus* have toe pads (and are frequently mistaken for hylids by the uninitiated herpetologist) and are usually semi-arboreal or arboreal in habits. Both *Hylactophryne* and *Ischnocnema* are terrestrial frogs; the former lives in arid, non-forested regions and the latter lives in moist, forested environments.

Hylactophryne and *Ischnocnema* may represent relicts of a formerly widespread eleutherodactyline stock from which more successful genera *(Eleutherodactylus)* evolved. At present, too little is known of the osteology of *Eleutherodactylus* to determine the evolutionary directions.

Niceforonia Goin and Cochran, 1963
(Fig. 104)

Niceforonia Goin and Cochran, 1963, Proc. California Acad. Sci., 31:499 [Type-species by original designation, *Niceforonia nana* Goin and Cochran, 1963].

Diagnostic definition.—7) omosternum moderate-sized; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, relatively broad at base; 11) palatal shelf of premaxilla broad, deeply notched; 12) facial lobe of maxilla deep anteriorly, tapering posteriorly; 13) palatal shelf of maxilla broad, pterygoid process moderate-sized; 15) nasals small, narrowly separated medially; nasals in contact in *flavomaculata*; 16) nasals in contact with maxillae, not with pterygoids; 19) frontoparietals not ornamented, except in *flavomaculata*; 20) frontoparietals not fused with proötics; 22) epiotic eminences obsolete; 23) cristae paroticae broad, stocky; 24) zygomatic ramus of squamosal of moderate length, widely separated from maxilla; 25) otic ramus of squamosal long, expanded medially into small otic plate; 26) squamosal-maxillary angle about 55°; 27) columella present in most species, absent in *montia*, probably absent in *simonsii*; 28) prevomers toothed or not, entire, relatively large, separated medially; 29) palatines slender, separated medially; 30) sphenethmoid entire, extending anteriorly beyond anterior edge of nasals; 31) anterior ramus of parasphenoid broad, long, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, short, not overlapped laterally by median rami of pterygoids; 33) pterygoids small, median rami short, anterior rami relatively long, not reaching palatines; 34) occipital condyles relatively small, stalked, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes on hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 42) males with large median subgular vocal sac; 43) body lacking glands; 44) tongue large, round, free at posterior edge; 45) toes lacking webbing and lateral fringes, digital tips narrow; 46-48); 49) adults small, less than 30 mm. SVL; 50) tympanum visible externally, concealed, absent *(montia)*, or possibly absent *(simonsii)*.

Composition.—Lynch (1968d) in-

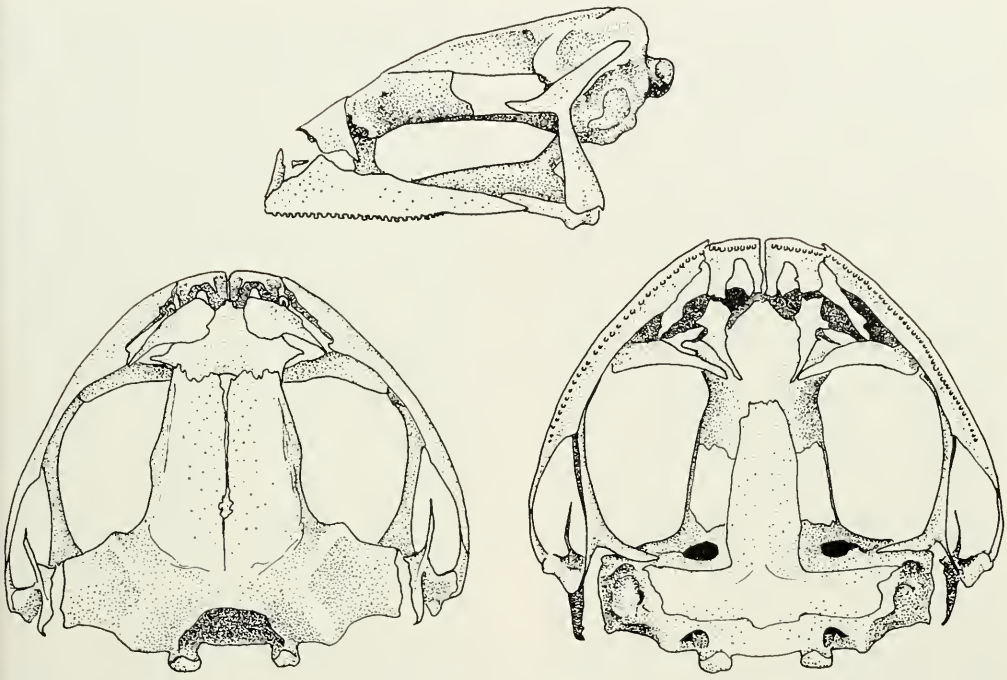

FIGURE 104. Lateral, dorsal, and ventral views of skull of *Niceforonia montia* (MCZ 24352, × 5).

cluded *N. nana, N. festae,* and *N. montia* as definite members of the genus and referred *N. columbiana* and *N. simonsii* to the genus. Based on examination of paratypes of *Eupsophus wettsteini* by stereo-radiographs, I now include that species in *Niceforonia. Eleutherodactylus flavomaculatus* Parker is a *Niceforonia* (Lynch, 1969b) and Cei's (1968b) *Syrrhophus laplacai* is probably a member of *Niceforonia* as well.

Distribution.—High elevations in the Andes of Colombia, Ecuador, Peru, and Bolivia.

Remarks.—Goin and Cochran (1963) considered *Niceforonia* to be most closely allied to *Eupsophus.* In external characters, *Eupsophus* and *Niceforonia* cannot be separated. The cervical cotylar arrangement and the median separation of the occipital condyles suggests that *Niceforonia* is more closely related to the Eleutherodactylini than to the Alsodini. The breeding biology of *Niceforonia* is unknown except that *N. flavomaculata* lays large terrestrial eggs, but the large eggs are suggestive of direct development in all of the species of the genus. The very distinctive sphenethmoid of *Niceforonia* is duplicated by at least one species of *Eleutherodactylus (bogotensis). Niceforonia* is separated from *Eleutherodactylus* because the digital tips are narrow, there is no terminal transverse groove on the digital tips, and the terminal phalanges are knobbed. The slight median separation of the nasal bones in *Niceforonia* occurs in several groups of *Eleutherodactylus,* although the trait is uncommon in *Eleutherodactylus.* The other eleutherodactylines with knobbed terminal phalanges *(Amblyphrynus, Holoaden, Hylactophryne,* and *Ischnocnema)* are distinctive when compared with *Niceforonia,* although *Holoaden* resembles *Niceforonia* in the arrangement of the cranial bones. This osteological similarity possibly reflects convergence in view of the dissimilar morphology of the hyoid plates of these two genera.

Sminthillus Barbour and Noble, 1920

(Fig. 105)

Sminthillus Barbour and Noble, 1920, Bull. Mus. Comp. Zool., 63:402 [Type-species by original designation, *Phyllobates limbatus* Cope, 1862].

Diagnostic definition.—7) omosternum small, elongate; 9) maxillary arch edentate; 10) alary processes of premaxillae directed dorsolaterally, short, broad at base; 11) palatal shelf broad, deeply dissected; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla of moderate width, no pterygoid process; 15) nasals small, narrowly separated medially; 16) nasals in tenuous contact with maxillae, separated from pterygoids; 19) frontoparietals not ornamented; 20) frontoparietals fused to proötics; 22) epiotic eminences present, small; 23) cristae paroticae very broad, stocky; 24) zygomatic ramus of squamosal very short, knobbed; 25) otic ramus of squamosal very long, no otic plate; 26) squamosal-maxillary angle about 60°; 27) columella present; 28) prevomers minute, greatly reduced in size, entire, widely separated medially; 29) palatines slender, widely separated medially, lateral to prevomers; 30) sphenethmoid entire, extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid narrow, not keeled medially; 32) parasphenoid alae slightly deflected posteriorly, very short, not overlapped laterally by median rami of pterygoids; 33) pterygoids very small, median and posterior rami short, anterior rami relatively long, extending to middle of orbit; 34) occipital condyles small, stalked, widely separated medially; 36) terminal phalanges T-shaped; 37) hyoid plate lacking alary processes; 40) *m. depressor mandibulae* in two slips; 42) males with median subgular vocal sac; 43) body lacking glands; 44) tongue narrow, posterior one-third free; 45) toes lacking webbing and lateral fringes, digital tips bear pads;

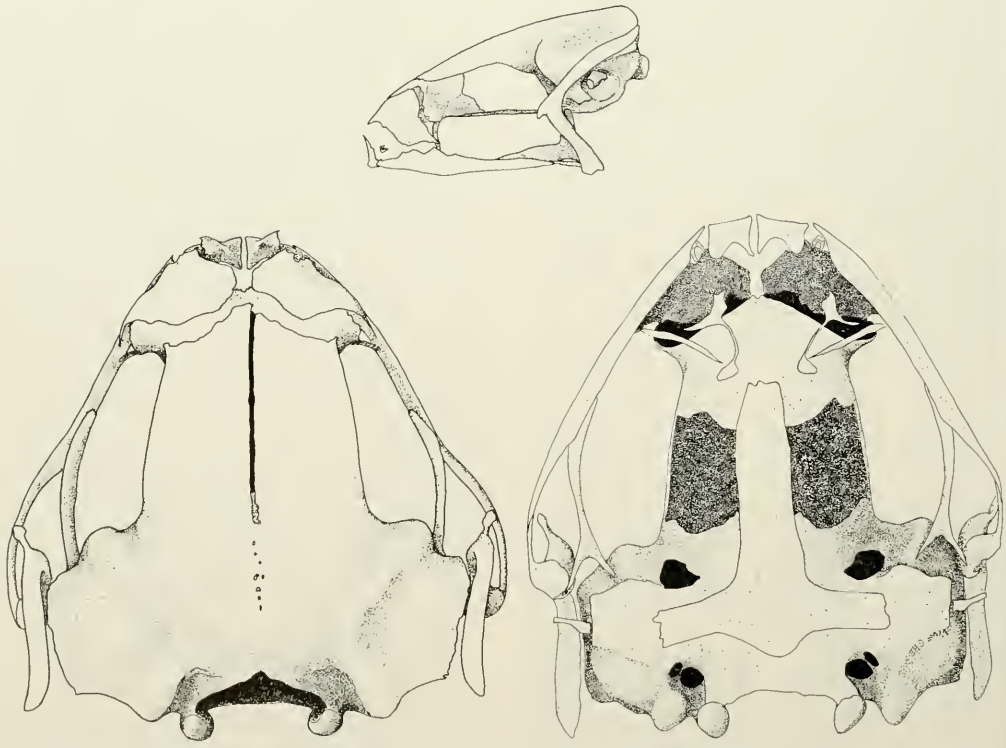

FIGURE 105. Lateral (× 7.5), dorsal, and ventral views of skull of *Sminthillus limbatus* (KU 68684, × 23).

49) adults small, less than 15 mm. SVL; 50) tympanum visible externally.

Composition.—Monotypic *(S. limbatus)* with two subspecies.

Distribution.—Cuba.

Remarks.—*Sminthillus* is closely related to the West Indian species of *Eleutherodactylus* and is most similar to the *E. auriculatus* group or to the *E. dimidiatus* group (as defined by Shreve and Williams, 1963). *Sminthillus* differs from the Alpha division of *Eleutherodactylus* in two characters—the loss of teeth and the loss of the alary processes of the hyoid plate. Barbour and Noble (1920) considered *Sminthillus* a dendrobatid or ranoid derivative, but Griffiths (1959) demonstrated that the genus was closely related to *Eleutherodactylus,* an opinion often voiced by Noble (e.g., 1931).

Sminthillus was named by Barbour and Noble (1920) on the basis of a partial epicoracoidal fusion. However, the fusion is not as great as maintained by Noble (1926a, 1931) and occurs in many more frogs than he believed. I consider the presence of the fusion to reflect more accurately the care of a dissection than morphological divergence. The other two species named in *Sminthillus* are now placed in other genera—the Peruvian species *(peruvianus)* is placed in the Beta division of *Eleutherodactylus* (see pp. 148-149) and the Brasilian species *(brasiliensis)* is the only species of the genus *Euparkerella.*

Syrrhophus Cope, 1878
(Fig. 106)

Epirhexis Cope, 1866, J. Acad. Nat. Sci. Philadelphia, 6:96 [Type-species by original designation, *Batrachyla longipes* Baird, 1859; suppression of the generic name requested by Lynch, 1967].

Syrrhophus Cope, 1878, Amer. Nat., 12:253 [Type-species by monotypy, *Syrrhophus marnockii* Cope, 1878].

Malachylodes Cope, 1879, Proc. Amer. Philos. Soc., 18:264 [Type-species by monotypy, *Malachylodes guttilatus* Cope, 1879].

Syrrhopus Boulenger, 1888, Proc. Zool. Soc. London, p. 206 [Emendation of *Syrrhophus* Cope, 1878].

Syrrhaphus Günther, 1901, Biol. Cent.-Amer., Rept. and Batr., p. 215 [Emendation of *Syrrhophus* Cope, 1878; hence taking same type-species *(marnockii)* and not *verruculatus* as claimed by Gorham (1966)].

Diagnostic definition.—7) omosternum moderate-sized; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, relatively narrow at base; 11) palatal shelf of premaxilla broad, deeply dissected; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla broad anteriorly, narrowing posteriorly, no pterygoid process; 15) nasals large, in broad median contact; 16) nasals not in contact with maxillae or pterygoids; 19) frontoparietal not ornamented; 20) frontoparietal fused to proötic; 22) epiotic eminences obsolete; 23) cristae paroticae short, broad; 24) zygomatic ramus of squamosal very slender, relatively short; 25) otic ramus of squamosal elongated, not forming otic plate; 26) squamosal-maxillary angle about 65°; 27) columella present; 28) prevomers reduced in size, dentigerous ramus lost, widely separated medially, or dentigerous rami present, bearing a few teeth; 29) palatines narrow, separated medially, in contact with maxillae; 30)

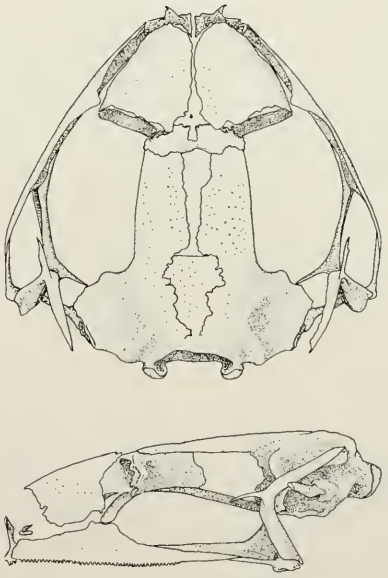

FIGURE 106. Lateral and dorsal views of skull of a male *Syrrhophus pipilans* (KU 59950, × 4).

sphenethmoid entire, extending anteriorly beneath posterior edge of nasals; 31) anterior ramus of parasphenoid broad, not keeled medially; 32) parasphenoid alae deflected posteriorly, short, widely separated from median rami of pterygoids; 33) pterygoids slender, all rami short; 34) occipital condyles small, not stalked, widely separated medially; 36) terminal phalanges T-shaped; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 42) males with or without large median subgular vocal sac; 43) axillary and/or inguinal glands present; 44) tongue narrow to relatively broad and rounded, posterior edge free; 45) toes lacking webbing, bearing lateral fringes or not, digital tips very slightly to broadly dilated into pads; 49) adults 16-40 mm. SVL; 50) tympanum concealed or visible externally.

Composition.—Lynch (1970a) recognized 12 species, two of which are polytypic: *cystignathoides, dennisi, guttilatus, interorbitalis, leprus, longipes, marnockii, modestus, nivocolimae, pipilans, rubrimaculatus,* and *verrucipes.*

Distribution.—Discontinuous in the Pacific lowlands from Sinaloa, México, to El Salvador, also in the eastern lowlands of México from the Edwards Plateau of Texas to British Honduras. Highland species occur along the Sierra Madre Oriental up to 2000 meters.

Remarks.—Lynch (1968a, 1970a) discussed the generic separation of *Eleutherodactylus, Syrrhophus,* and *Tomodactylus.* In external characters, *Syrrhophus* is not separable from all *Eleutherodactylus.* The osteological peculiarities of *Syrrhophus* are duplicated by *Tomodactylus* and the Alpha division of *Eleutherodactylus. Syrrhophus* and *Tomodactylus* are distinguished in some external characters (lumbar gland, arrangement of the supernumerary plantar tubercles) and by one paedomorphic skeletal character—the sphenethmoid is usually divided in *Tomodactylus* and is entire in *Syrrhophus.* The division of the sphenethmoid is a paedomorphic feature and therefore should not be given undue weight in any classification. The separation of *Syrrhophus* and *Tomodactylus* as distinct genera is a debatable point, and I retain them as generically distinct only as a matter of convenience. The character of the glands used by Lynch (1968a) to separate the two genera tends to be less diagnostic when the species of the two genera from northwestern México are compared *(S. interorbitalis, S. modestus, T. saxatilis).*

Until a comprehensive revision of the genus *Eleutherodactylus* is completed and the skeletons of the majority of species studied, it will not be possible to argue definitively whether the genera *Syrrhophus* and *Tomodactylus* are derivatives of the Alpha or the Beta divisions of *Eleutherodactylus.* In an attempt to clarify this point, I studied representatives of all species groups of Central American *Eleutherodactylus* and found no group which exhibits the osteological characteristics of the Alpha division. If *Syrrhophus* and *Tomodactylus* were derivatives of the South American groups of the Alpha division, one might expect some relict species to be distributed in parts of Lower Central America. However, all Central American species of *Eleutherodactylus* examined by me are Beta division *Eleutherodactylus,* as are those species of the genus found in the Chocó of Colombia and Ecuador. Therefore I suggest that the Mexican *Syrrhophus* and *Tomodactylus* are more closely related to the West Indian *Eleutherodactylus* (Alpha division) than to any other groups of the genus. Within the Alpha division, the *auriculatus* group most closely approaches the morphology of the endemic Mexican eleutherodactyline genera *Syrrhophus* and *Tomodactylus.*

Tomodactylus Günther, 1901
(Fig. 107)

Tomodactylus Günther, 1901, Biol. Centr.-Amer., Rept. and Batr., p. 219 [Type-

species by monotypy, *Tomodactylus amulae* Günther, 1901].

Diagnostic definition.—7) omosternum moderate-sized; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, broad at base; 11) palatal shelf of premaxilla narrow, palatal process elongate; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla narrow, pterygoid process moderate-sized; 15) nasals large, in broad median contact; 16) nasals not in contact with maxillae or pterygoids; 18) frontoparietal fontanelle absent in adults, often present in young males; 19) frontoparietals not ornamented; 20) frontoparietal fused to proötic; 22) epiotic eminences obsolete; 23) cristae paroticae short and stocky; 24) zygomatic ramus of squamosal sliver-like, very short; 25) otic ramus of squamosal very long, no otic plate; 26) squamosal-maxillary angle 50-60°; 27) columella present; 28) prevomers reduced in size, edentate, widely separated medially; 29) palatines slender, widely separated medially; 30) sphenethmoid usually divided, not extending anteriorly to nasals; 31) anterior ramus of parasphenoid relatively broad, not keeled medially; 32) parasphenoid alae deflected posteriorly, short, not overlapped by median rami of pterygoids; 33) pterygoids slender, all rami short; 34) occipital condyles small, not or but slightly stalked, widely separated medially; 36) terminal phalanges T-shaped; 37) alary processes of hyoid plate on narrow stalks; 40) *m. depressor mandibulae* in two slips; 42) males with large, median, subgular vocal sac; 43) lumbar gland usually well defined, axillary glands sometimes present; 44) tongue relatively small, narrow, posterior edge free; 45) toes lacking webbing, digital tips slightly to broadly dilated; 49) adults 21-31 mm. SVL; 50) tympanum visible externally.

Composition.—The genus was revised by Dixon (1957) and two species were subsequently named. Nine species are presently recognized: *albolabris, angustidigitorum, dilatus, fuscus, grandis, niti-*

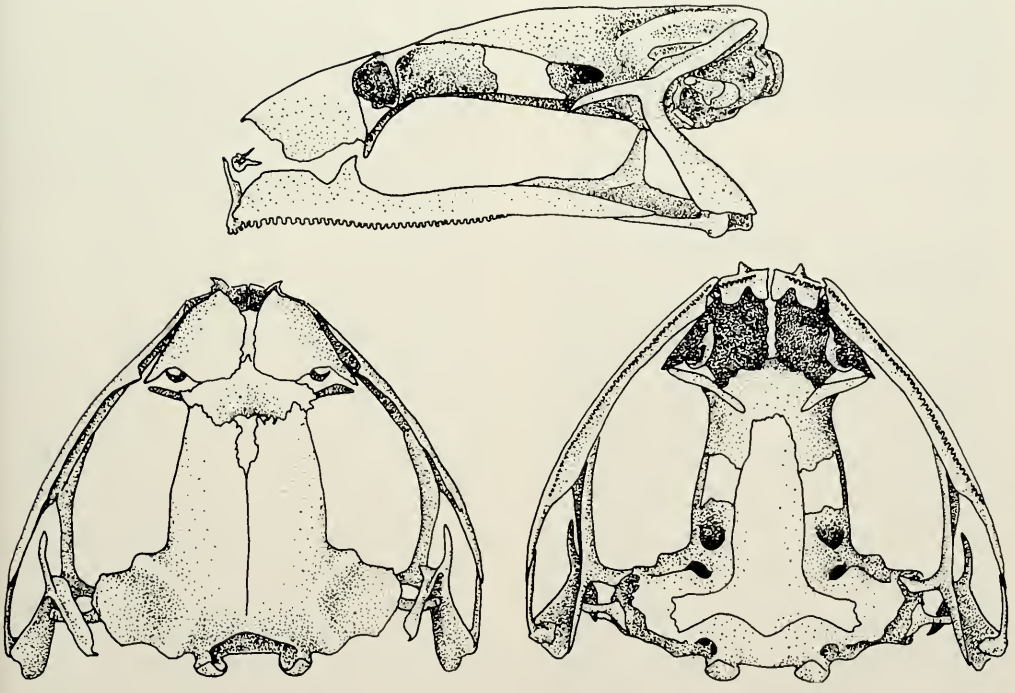

FIGURE 107. Lateral, dorsal, and ventral views of skull of a female *Tomodactylus nitidus* (KU 102649, × 4.7).

dus (3 subspecies), *rufescens, saxatilis,* and *syristes.* Dixon and Webb (1966) briefly commented on an unnamed species from Nevado de Colima, Jalisco, México.

Distribution.—The Cordillera Volcánica of México from western Veracruz to Colima; the Oaxacan Plateau, the Sierra Madre del Sur of Oaxaca and Guerrero, and the Pacific lowlands from Sinaloa to Michoacán. The genus is largely allopatric to *Syrrhophus.*

Remarks.—Gallardo (1965) placed *Tomodactylus* in the Leptodactylinae and *Syrrhophus* and *Eleutherodactylus* in the Eleutherodactylinae. This association was based on erroneous data concerning the breeding biology of *Tomodactylus.*

Tomodactylus is primarily a lower montane genus, whereas the closely related *Syrrhophus* is primarily a lowland genus (Lynch, 1970a), but the two genera are sympatric in the lowlands of western México. The differences between them are expressed to the greatest degree in eastern and southern México and expressed to a lesser degree in western México, suggesting that the generic dichotomy occurred in western México.

Tribe *incertae sedis*

Scythrophrys new genus

Type-species.—Zachaenus sawayae Cochran, 1953.

The following characteristics of the *diagnostic definition* are observable: 1) sternum cartilaginous; 2) vertebral shield lacking; 6) cranial bones not dermostosed; 7) omosternum small; 8) sacral diapophyses rounded; 9) maxillary arch toothed, teeth blunt, pedicellate; 14) maxillary arch complete; 18) frontoparietal fontanelle lacking; 21) temporal arcade lacking; 24) zygomatic ramus of squamosal relatively long, widely separated from maxilla; 28) prevomers toothed, dentigerous processes large, transversely elongate, situated posterior to choanae; 36) terminal phalanges apparently knobbed; 40) *m. depressor mandibulae* in two slips, *pars tympanicus* very large, *p. scapularis* minute; 41) pupil horizontal; 43) body lacking glands; 44) tongue relatively large, posterior edge free; 45) toes lacking webbing but have lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged or spade-like, digital tips narrow on fingers, those of toes slightly dilated, thumb very short; 49) single adult female known is 16.9 mm. SVL; 50) tympanum concealed.

Etymology.—Greek, *scythros* + *phryne,* meaning "sullen toad."

Remarks.—A single specimen of this southeastern Brasilian frog is known; it was named as a member of *Zachaenus* by Cochran (1953). In external appearance, the frog resembles *Physalaemus* (*maculiventris* group) or *Paratelmatobius* and, in some respects, *Zachaenus.* Cochran (1953) considered the small tubercles on the upper eyelid as indicative of some relationship with *Zachaenus* but noted the many points of disagreement between *parvulus* and *sawayae.* The most striking difference between the two species is seen in the length and shape of the fingers (Fig. 94). The very short thumb of *Scythrophrys* is suggestive of a reduced phalangeal formula for the hand. The tympanum is recessed and smaller than indicated by Cochran (1953).

Scythrophrys is placed with confidence in the Telmatobiinae but is not assigned to any tribe, because many characters are not known. Based on the available information, I consider the genus to belong either to the Grypiscini or Eleutherodactylini, but until the osteology and breeding biology of *Scythrophrys* are known, definite assignment to a tribe would be presumptuous.

Cochran's (1953) description of the holotype (USNM 125530) is relatively accurate. My measurements of the holotype differ somewhat from hers, reflecting either differences in techniques or possibly shrinkage. I recorded the fol-

lowing measurements (in millimeters): snout-vent length 16.9, shank length 8.4, head width 6.3, head length 5.6, eye length 1.9, eyelid width 1.7, and interorbital distance 2.6. A few cranial characters are visible through a small tear in the skin of the head. The frontoparietals are broad and a fontanelle is lacking. The nasals appear to be relatively large and in median contact. Two characters of the foot were not mentioned by Cochran. There is a small calcar on the heel and a narrow outer tarsal fold extending for the length of the tarsus onto the fifth toe.

Elosiinae Miranda-Ribeiro, 1926

Elosiidae Miranda-Ribeiro, 1926:27.
Elosiinae: Noble, 1931:504. Gallardo, 1965: 84.

Miranda-Ribeiro (1926) proposed the Elosiidae for three genera; the concept and content of the group has remained unchanged since its proposal. Three genera are presently included in the subfamily: *Crossodactylus, Hylodes (=Elosia auctorum),* and *Megaelosia.* Cochran (1938) named *Crossodactylodes,* which she considered possibly related to the elosiines. She thought that the digital morphology of *Crossodactylodes* indicated that the genus exhibited primitive elosiine characters. The apparent dorsal dermal glands on the digital pads of *Crossodactylodes* are artifacts reflecting the Y-shaped terminal phalanges. Goin and Cochran (1963) suggested that *Trachyphrynus* was related to *Crossodactylus.* I previously discussed this point and placed *Trachyphrynus* in the synonymy of *Eleutherodactylus* (Lynch, 1968d).

Noble (1922, 1931) considered the Elosiinae to be a bufonid group. The subfamily was associated with the Leptodactylidae by Davis (1936), who pointed out that the Bufonidae and Leptodactylidae could be familially distinguished. The type-genus of the subfamily, *Elosia* Tschudi, 1838, is a synonym of *Hylodes* Fitzinger, 1826 (which is not to be confused with *Hylodes* Fitzinger, 1843, which is a synonym of *Eleutherodactylus* Duméril and Bibron, 1841). The family-group name need not be changed simply because the type-genus is a synonym (see Article 40, International Code of Zoological Nomenclature, 1961). At any rate, the family-group name could not be changed so as to be based on *Hylodes* Fitzinger, 1826, because Günther (1859a) proposed a Hylodidae based on *Hylodes* Fitzinger, 1843.

Until recently, the subfamily was known only from southeastern Brasil and Misiones Province, Argentina, but it is now known to occur also in Venezuela (Cerro Duida, Guiana Massif). The subfamily is homogeneous morphologically and is readily distinguished from all other leptodactylid groups. The following diagnostic characters are common to the three genera of the Elosiinae: 1) sternum cartilaginous, tending to calcify in old adults; 2) vertebral shield lacking; 3) transverse processes of anterior presacral vertebrae short, those of posterior presacral vertebrae also shortened; 4) cervical cotylar arrangement type I; 5) cervical and second vertebrae not fused; 6) cranial bones not involved in dermostosis; 7) omosternum present, moderate-sized; 8) sacral diapophyses rounded; 9) maxillary arch toothed, teeth pointed, pedicellate; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla narrow, no pterygoid process; 15) nasals small, widely separated medially; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals not ornamented; 21) temporal arcade lacking; 23) carotid artery passes dorsal to skull bones; 27) columella present; 30) sphenethmoid very large, entire, extending anteriorly to anterior edge of nasals; 36) terminal phalanges T-shaped; 37) alary processes of hyoid plate on narrow stalks; 38) cricoid cartilage not divided ventrally; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral

edge of hyoid plate; 40) *m. depressor mandibulae* in two slips; 41) pupil horizontal; 43) body lacking glands; 44) tongue large, not notched, posterior edge free; 45) toes bearing large lateral fringes, large flap-like tarsal fold present, outer metatarsal tubercle present, inner metatarsal tubercle not spade-like, digital tips broad; 46) larvae with 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 47) amplexus axillary in known species; 48) eggs small, numerous, laid in moist terrestrial situations or in ponds or streams; 50) tympanum visible externally; 51) each digital pad has a pair of dermal, scute-like glandular pads on dorsal surface. The vertebral arches of all elosiines are very nonimbricate and the vertebrae and coccyx are poorly ossified.

The Elosiinae are of particular interest in that the poison-arrow frogs (Dendrobatidae) are apparently derived from this leptodactylid subfamily. The two groups agree in cranial morphology, vertebral columns, the T-shaped terminal phalanges, the dermal glandular pads on top of the digital pads, and in the presence, in at least some species of each group, of toxic skin secretions (the secretions of the elosiines have not been chemically analyzed). The two groups differ in breeding biology and in the architecture of the pectoral girdle.

Crossodactylus best fits my concept of the primitive elosiine but has diverged in at least one character—the loss of the quadratojugal. The genus is distinctive in its ranoid pattern of the attachment of the distal tendons of the thigh musculature. The ranoid pattern of the thigh musculature of *Crossodactylus* is exactly like that seen in the dendrobatids and mitigates the importance of one of the criteria used by Griffiths (1963) to associate the dendrobatids as a Neotropical subfamily of the Ranidae. *Crossodactylus* has a median subgular vocal sac and nuptial asperities (cluster of spines) in the males. This condition is like that seen in most Telmatobiinae (excepting the Eleutherodactylini which lack nuptial asperities); I regard the presence of vocal sac and nuptial asperities as primitive. The tadpoles of *Crossodactylus* have median vents in contrast to the dextral vents of the tadpoles of *Hylodes* and *Megaelosia*. *Hylodes* and *Megaelosia* have the bufonid pattern of the arrangement of the distal tendons of the thigh musculature, derived conditions of the vocal apparatus, and quadratojugal bones. I envision the dendrobatids as having diverged from the *Crossodactylus* stock prior to the loss of the quadratojugal, but after *Hylodes* and *Megaelosia* had evolved.

Crossodactylus Duméril and Bibron, 1841

(Fig. 108)

Crossodactylus Duméril and Bibron, 1841, Érpetologie généralé, 8:635 [Type-species by monotypy, *Crossodactylus gaudichaudii* Duméril and Bibron, 1841].

Limnocharis Bell, *in* Darwin, 1843, Zool. Voyage Beagle, Reptiles, 5:33 [Type-species by monotypy, *Limnocharis fuscus* Bell, 1843].

Tarsopterus Reinhardt and Lütken, 1862, Vid. Meddel. Naturh., Foren., 1861:177 [Type-species by monotypy, *Tarsopterus trachystomus* Reinhardt and Lütken, 1862].

Calamobates DeWitte, 1930, Miss. Biol. Belge Bresil, 2:219 [Type-species by monotypy, *Calamobates boulengeri* DeWitte, 1930].

Diagnostic definition.—10) alary processes of premaxillae directed anterodorsally and laterally, broad at base; 11) palatal shelf of premaxilla narrow, palatal process elongate; 14) maxillary arch incomplete, maxilla tapering posteriorly, quadratojugal absent; 16) nasals separated from both maxillae and pterygoids; 20) frontoparietal fused to proötic; 22) epiotic eminences moderately distinct; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal of moderate length, pointed, widely separated from maxilla; 25) otic ramus of squamosal slightly shorter than zygomatic ramus, no otic plate; 26) squamosal-maxillary angle about 50°; 28) prevomers moderately small, separated medially, dentigerous ramus lost

or not, rarely toothed; 29) palatines small, narrow, widely separated medially; 31) anterior ramus of parasphenoid short, broad, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, short, widely separated from median rami of pterygoids; 33) pterygoids with slender rami, anterior rami not reaching palatines; 34) occipital condyles small, stalked, widely separated medially; 35) mandible lacking odontoids; 42) males with median, subgular vocal sac, nuptial spines in a cluster in all species; 46) larvae with median vent; 49) adults relatively small, less than 40 mm. SVL.

Composition.—Six species are presently recognized *(aeneus, dispar, gaudichaudii, grandis, schmidti,* and *trachystoma),* although some authors favor regarding *dispar* and *grandis* as conspecific. The most recent revision of the genus (Cochran, 1955) did not treat *C. grandis* B. Lutz, 1951, or *C. schmidti* Gallardo, 1961.

Distribution.—Southeastern Brasil in the lowlands from southern Minas Geraís to Misiones Province, Argentina.

Remarks.—The generic synonymy of *Crossodactylus* has been stable for many years. Cochran (1955) and Gallardo (1961) presented studies of intrageneric variation and relationships. *Crossodactylus* is primitive to the other elosiines in tadpole morphology (median vent) and in the secondary sex characteristics (median subgular vocal sac and nuptial asperities), but is specialized in the loss of the quadratojugal. *Hylodes* is similar to *Crossodactylus* in having a poorly ossified quadratojugal, but differs from *Crossodactylus* in the other characteristics mentioned.

The ranoid pattern of the attachment of the distal tendons of the thigh musculature of *Crossodactylus* distinguishes the genus from the other elosiines, as well as from all other Neotropical leptodactylids. The thigh musculature of *Crossodactylus* adds yet another character to the impressive list of characters shared by the dendrobatids and *Crosso-*

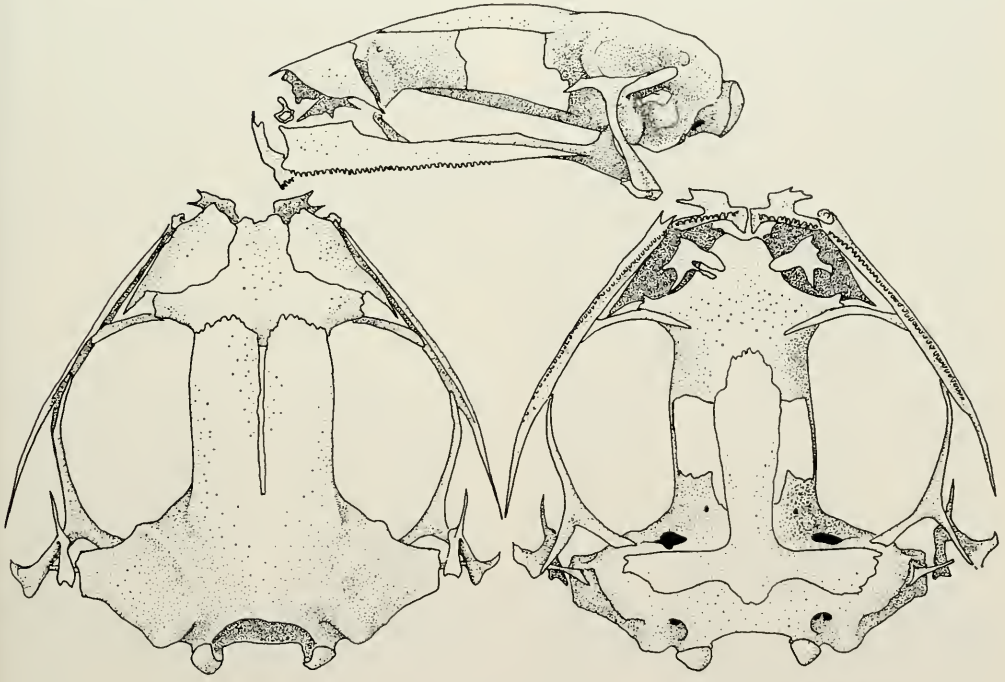

FIGURE 108. Lateral, dorsal, and ventral views of skull of *Crossodactylus gaudichaudii* (KU 92759, × 4.7).

dactylus. Noble (1931) argued that the Dendrobatinae were derived from the bufonid genus *Crossodactylus,* because he found the digital pad structure of the two groups to be identical and to exist in no other Neotropical bufonoid frogs. Noble argued that the condition of the epicoracoidal cartilages of *Crossodactylus* is precursorial to the condition seen in developing *Phyllobates (=Colostethus) subpunctatus.* Noble considered his data adequate to demonstrate that the firmisternal dendrobatids passed through an arciferal condition in ontogeny. Griffiths (1959, 1963) sought to ally the dendrobatids with ranids and argued that the dendrobatids do not pass through an arciferal stage in development. The developmental pattern of the pectoral girdle exhibited by *Colostethus subpunctatus* is clearly ranoid. My own study of this subject completely supports that of Griffiths.

Griffiths (1963) rejected Noble's argument that the thigh musculature was of primary importance in anuran classification, but cited the thigh musculature as additional evidence supporting his contention that dendrobatids are a ranid subfamily. Griffiths cited the similar development of the digital pads of the Petropedetinae (Ranidae) as supportive evidence for the close relationship between the dendrobatids and ranids. His argument requires that we ignore the many similarities between elosiines and dendrobatids and regard several character complexes as evolving in a parallel fashion in leptodactylids and ranids. Associating the dendrobatids with the bufonoids requires that we regard the firmisternal pectoral girdles of dendrobatids and ranids to have been independently evolved. This position is made less objectionable by the occurrence of a nearly complete transition from arcifery to firmisterny within the Neotropical Bufonidae. Noble's (1922) position that the firmisternal pectoral girdle has appeared more than once is regarded as correct.

Griffiths (1963) cited several other characters as exclusively ranoid. The *bursa angularis oris* is not restricted to dendrobatids and ranids as Griffiths stated but occurs in most, if not all, groups of advanced frogs (Baldauf and Tanzer, 1965, Trueb, 1966, 1968, 1970, and Starrett, 1968).

The dendrobatids are amply distinct from the elosiine leptodactylids. I do not intend to present an argument that the two families ought to be combined, because I think that there is value in recognizing the small, brightly colored, poisonous Neotropical dendrobatid frogs as familially distinct. The dendrobatids have lost the palatines, which are retained, although they are small, in elosiine leptodactylids. The firmisternal architecture of the pectoral girdle of dendrobatids is markedly different from the arciferal architecture exhibited by all leptodactylids. The breeding behavior and biology of the dendrobatids is not unique among frogs but is very different from that of the elosiine leptodactylids. Dendrobatid tadpoles usually have 2/3 tooth rows, although several species have reduced numbers (Starrett, 1960). The tadpoles of all dendrobatids have a broad anterior interruption of the labial papillae as do most leptodactylids. *Dendrobates* has either a median or dextral vent, whereas all known tadpoles of *Colostethus* and *Phyllobates* have dextral vents.

Hylodes Fitzinger, 1826

(Fig. 109)

Hylodes Fitzinger, 1826, Neue Class. Rept., p. 38 [Type-species by monotypy, *Hylodes ranoides* (=*Hyla ranoides* Spix, 1824)].

Enydrobius Wagler, 1830, Nat. Syst. Amph., p. 202 [Substitute name for *Hylodes* Fitzinger, 1826; hence taking same type-species].

Elosia Tschudi, 1838, Classif. Batr., p. 77 [Type-species by monotypy, *Elosia nasuta* Tschudi, 1838].

Scinacodes Fitzinger, 1843, Syst. Rept., p. 32 [Type-species by original designation, *Hyla nasus* Lichtenstein, 1823].

Diagnostic definition.—10) alary processes of premaxillae directed anterodor-

sally and laterally, broad at base; 11) palatal shelf of premaxilla relatively narrow, palatal process relatively small; 14) maxillary arch complete, quadratojugal poorly ossified; 16) nasals not in contact with maxillae or pterygoids; 20) frontoparietals fused to proötics; 22) epiotic eminences moderately distinct; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal short, truncate, widely separated from maxilla; 25) otic ramus of squamosal about as long as zygomatic ramus, not expanded into otic plate; 26) squamosal-maxillary angle about 40°; 28) prevomers entire, toothed, separated medially; 29) palatines long, narrow, widely separated medially; 31) anterior ramus of parasphenoid short, broad, keeled medially in at least some species; 32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; 33) pterygoids relatively small, rami slender, anterior rami elongate, reaching palatines; 34) occipital condyles small, not stalked, widely separated medially; 35) mandible lacking odontoids; 42) males with paired, lateral, membranous vocal sacs, absent in one species, and with nuptial asperities in a pad on thumb; 46) larvae with dextral vent; 49) adults 30-45 mm. SVL.

Composition.—Bokermann (1966) listed nine species *(aspera, glabrus, lateristrigatus, magalhaesi, mertensi, meridionalis, nasus, perplicatus,* and *pulcher)* in the genus, then known only from southeastern Brasil. Gorham (1966) listed *glabrus* as a synonym of *lateristrigatus* and *meridionalis* as a subspecies of *nasus.* Bokermann (1967) named an additional species from Rio de Janeiro *(ornata),* and Rivero (1968) named *duidensis* from Venezuela. All of these authors used the generic name *Elosia,* as did Cochran (1955) in her study of the species of southeastern Brasil.

Distribution.—Coastal southern and southeastern Brasil from Rio Grande do Sul north to Minas Geraís. One species occurs on Cerro Duida in Amazonian Venezuela.

Remarks.—Frogs of this genus exhibit relatively little intrageneric variation and have been recognized as a distinctive generic unit for many decades.

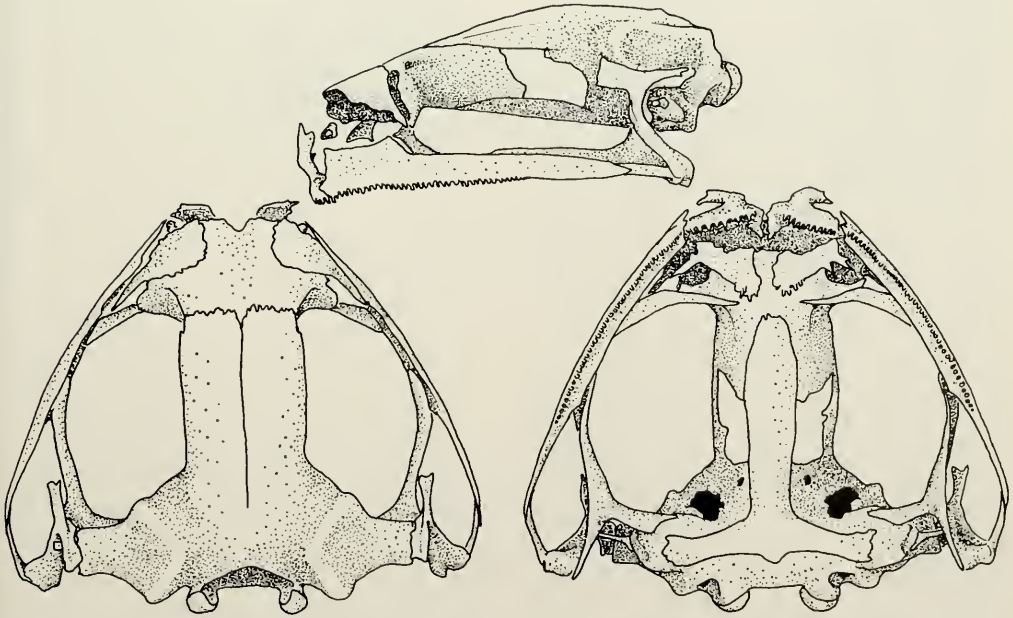

FIGURE 109. Lateral, dorsal, and ventral views of skull of *Hylodes asper* (KU 92870, × 4).

The nomenclatorial problems of the genus are by no means minor. Myers (1962) pointed out that the proper generic name for these frogs is *Hylodes* Fitzinger, 1826, and not *Elosia* Tschudi, 1838, the name which had been applied more or less universally for 60 years. The usage of one generic name in preference to another in a significant work must be taken into account when dealing with any question of priority and/or nomenclatorial stability. It is therefore significant that Cochran (1955) used *Elosia* in her important study of the frogs of southeastern Brasil. However, the argument against usage of *Hylodes* as the proper generic name is based on the fact that Fitzinger proposed *Hylodes* twice, each time with a different type-species. Fitzinger (1826) proposed *Hylodes* for *Hyla ranoides* Spix, 1824, a member of the group later named *Elosia* by Tschudi (1838), and in 1843 proposed *Hylodes* for *Hylodes martinicensis* Tschudi, 1838, the type-species of *Eleutherodactylus* Duméril and Bibron, 1841. I am in complete agreement with Myers (1962), because there is no longer any confusion of what *Hylodes* is—the last author to use it in the sense of Fitzinger (1843) was Melin (1941). We have used *Eleutherodactylus* as the proper generic name since the early part of this century when Stejneger (1904) pointed out the synonymies of Fitzinger's names. The genus *Hylodes* (or *Elosia*) is a small one; even the least conservative author would not recognize a dozen species. The genus is restricted in distribution, and the species of the genus are relatively rare and therefore have not been frequently mentioned in the literature. A nomenclatorial change at the generic level creates relatively little instability even when the generic name used is one that has a junior homonym that is far better known. I do not regard the use of *Elosia* defensible while there are two older generic names *(Hylodes* and *Enydrobius)* for the group.

Megaelosia Miranda-Ribeiro, 1923
(Fig. 110)

Megaelosia Miranda-Ribeiro, 1923, Rev. Mus. Paulista, 13:819 [Type-species by monotypy, *Megaelosia bufonia* Miranda-Ribeiro, 1923].

Diagnostic definition.—9) maxillary teeth very long; 10) alary processes of premaxillae directed sharply posterodorsally; 11) palatal shelf of premaxilla of moderate depth, palatal process elongate; 14) maxillary arch complete, posterior end of maxilla expanded, quadratojugal present, deep; 16) nasals in contact with maxillae, separated from pterygoids; 20) frontoparietals not fused to proötics; 22) epiotic eminences obsolete; 23) cristae paroticae broad, stocky; 24) zygomatic ramus of squamosal long, expanded, in broad contact with maxilla; 25) otic ramus of squamosal relatively long, expanded medially into small otic plate; 26) squamosal-maxillary angle about 15°; 28) prevomers moderate-sized, entire, toothed; 29) palatines elongate, relatively broad, widely separated medially; 31) anterior ramus of parasphenoid elongate, narrow, not keeled medially; 32) parasphenoid alae deflected posteriorly, broadly overlapped laterally by median rami of pterygoids; 33) pterygoids large, anterior rami not reaching middle of orbits; 34) occipital condyles moderately large, not stalked, narrowly separated medially; 35) mandible bearing a serrated odontoid ridge; 42) males lacking vocal sac and nuptial asperities; 46) larvae with dextral vent; 49) males reach 70 mm., females reach 120 mm. SVL.

Composition.—Monotypic *(goeldi)*; the type-species of the genus is a junior synonym.

Distribution.—The Coastal Ranges of southeastern Brasil (Estados Rio de Janeiro and adjacent Minas Geraís and São Paulo).

Remarks.—Ever since its separation from *Hylodes (Elosia auctorum), Megaelosia* has been a poorly defined genus. Noble (1931) and Cochran (1955) re-

marked that *Megaelosia* was merely a giant *Elosia* with somewhat enlarged maxillary teeth. Cochran (1955) recognized the genus because of its greater adult size.

Megaelosia has diverged markedly from the other elosiines. The external morphology of *M. goeldi* compels me to retain it in the Elosiinae. The skull of this monotypic genus is strikingly different from those of the other genera of the subfamily (see Figs. 108-10). In contrast to the rather delicate maxillary arch in the other genera of the subfamily, *Megaelosia* has a large, massive maxilla and quadratojugal. The teeth of *Megaelosia* are fang-like and much larger than those of the other genera of the subfamily. The squamosal architecture of *Megaelosia* is very different from that seen in the other elosiines; the zygomatic ramus is enlarged and in broad contact with the maxilla, and the otic ramus of *Megaelosia* is more like that seen in the Grypiscini (Telmatobiinae) than that in *Hylodes* or *Crossodactylus*. The very large (compared to those of the other elosiines) occipital condyles of *Megaelosia* are suggestive that the genus is primitive. In external morphology, *Megaelosia goeldi* is very similar to *Hylodes*. The tadpoles of the two genera are very difficult to separate. These data suggest that the two genera are indeed related although the skull morphology suggests that the external similarities are convergent or parallel.

Leptodactylinae Berg, 1896 (1838)

Cystignathi Tschudi, 1838:78.
Cystignathidae: Günther, 1859a:26.
Pleurodemae Cope, 1866:95.
Paludicolina Mivart, 1869:290.
Plectromantidae Mivart, 1869:291.
Cystignathina: Mivart, 1869:293-94.
Leptodactylidae Berg, 1896:161 [A replacement name for the Cystignathidae, the type-genus of which is a synonym of *Leptodactylus*].
Cystignathinae: Gadow, 1901:211.
Paludicolidae: Miranda-Ribeiro, 1926:153.
Leptodactylinae: Noble, 1931:504.
Pseudopaludicolinae Gallardo, 1965:84.

The unifying characteristic of this subfamily is the bony style or osseous plate in the sternum as compared with the cartilaginous sterna of the other leptodactylids. The group is strictly Neo-

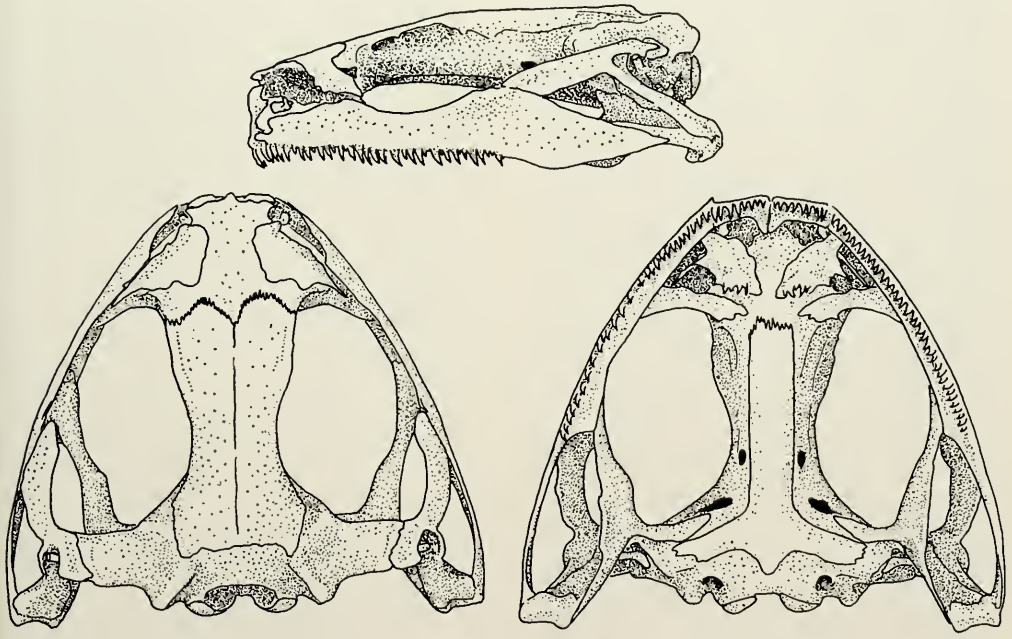

Figure 110. Lateral, dorsal, and ventral views of skull of *Megaelosia goeldi* (KU 106271, × 2.3).

tropical and ranges south to southern Chile and north to the southern United States. For the most part, the group is a lowland component. The widespread genus *Leptodactylus* rarely reaches elevations above 1000 meters. The genus *Pleurodema* occurs in the Andean system in Chile, Bolivia and southern Peru, and therefore reaches elevations exceeding 4000 meters. Even at these elevations, the group breeds in ponds. The pond-breeding habits of the Leptodactylinae have restricted the dispersal of the group to lower elevations. Many of the species of the subfamily are the wide-spread, common, lowland frogs encountered in most tropical situations in the Americas.

The following characteristics of the diagnostic definitions are common to all ten of the included genera: 1) sternum containing an osseous element; 2) vertebral shield lacking; 3) transverse processes of anterior presacral vertebrae not expanded or shortened; 5) cervical and second vertebrae not fused; 6) cranial bones not involved in dermostosis; 7) omosternum present; manubrium expanded in all genera except *Paratelmatobius* and *Physalaemus*; 9) maxillary arch usually toothed, if present, teeth blunt, pedicellate; 11) palatal process of premaxilla long; 20) frontoparietal not fused to proötic; 21) temporal arcade lacking; 23) carotid artery passes dorsal to skull bones; 24) zygomatic ramus of squamosal widely separated from maxilla; 30) sphenethmoid entire; 35) mandible lacking odontoids; 38) cricoid cartilage not divided ventrally; 40) *m. depressor mandibulae* in two slips; 44) posterior edge of tongue free; 45) outer metatarsal tubercle present; 47) amplexus axillary in all observed species.

Most herpetologists familiar with the Neotropical fauna have recognized two informal groups of aquatic breeding leptodactyline frogs—those associated with *Leptodactylus (Hydrolaetare, Leptodactylus, Limnomedusa,* and *Lithodytes)* and those long called "*Paludicola*" *(Engystomops, Eupemphix, Paratelmatobius, Physalaemus, Pleurodema,* and *Pseudopaludicola).* The rare genus *Edalorhina* is usually associated with the latter group but bears considerable resemblance to *Lithodytes.*

Boulenger (1882) was familiar with most of the generic groups here included in the Leptodactylinae. *Hydrolaetare* and *Paratelmatobius* were described subsequent to his studies. Boulenger included *Engystomops* and *Eupemphix* in the Bufonidae and incorrectly associated *Hylorina* with the Leptodactylinae, because he believed that *H. sylvatica* had a bony sternum. One of the genera recognized by Boulenger was *Paludicola,* which he considered to be wide-spread and generalized. Méhely (1904) and Parker (1927) pointed out the heterogeneity of Boulenger's *Paludicola* and each proposed a partitioning based on osteological characters. Méhely divided *Paludicola* into two genera—*Paludicola* and *Pleurodema.* Parker (1927) divided it into three genera—*Physalaemus, Pleurodema,* and *Pseudopaludicola.* Méhely separated Boulenger's *Paludicola* into one group with prevomerine teeth and a simple (non-bifurcate) sternal style *(Pleurodema)* and into another group without prevomerine teeth and with a bifurcate sternal style *(Paludicola).* Nieden (1923) uncritically followed Méhely's system and included *Edalorhina* in *Pleurodema.* Parker (1927) criticized Méhely's arrangement because relatively few species had been studied; he proposed another classification of the paludicoline frogs based on loss of the prevomerine teeth, loss of the quadratojugal, shape of the sternal style, and the presence of an antebrachial tubercle. Parker (1927) characterized *Pseudopaludicola* as having an elongate, cartilaginous, or calcified sternum. Virtually all subsequent authors have repeated Parker's characterization of the sternum of *Pseudopaludicola* (Barrio, 1954, Cochran, 1955, Rivero, 1961, and Gallardo, 1965). Principally on the basis of the cartilaginous sternum and breeding habits, Gal-

lardo (1965) proposed a new subfamily for *Pseudopaludicola*. In the present study, at least one specimen of each of five currently recognized species of *Pseudopaludicola* was cleared and stained. The sternal style is narrow and elongate and is much more dense than the epicoracoidal cartilages, but is not more dense than the coracoid bones. I consider the sternal style of *Pseudopaludicola* to be osseous. Parker (1927) reported simple and T-shaped terminal phalanges in frogs of the genus *Pseudopaludicola*. All specimens which I examined have knobbed terminal phalanges.

The foam-nesting habits of leptodactylines have been known for some time and have been used in the classification of the group (Noble, 1927, Breder, 1946, Bokermann, 1962). Barrio (1954) first reported the ethological differences between *Physalaemus* and *Pseudopaludicola*. *Pseudopaludicola* lays its eggs singly or in small clumps in water without the benefit of a foam-nest. The species of *Physalaemus* (including *Engystomops* and *Eupemphix*) lay their eggs in a foam-nest floating on water (Fig. 2). Frogs of the genus *Leptodactylus* also make foam-nests but there is considerable variation within the genus. The species of the *melanonotus* and *ocellatus* groups lay their eggs in a foam-nest floating on water, as do *Physalaemus* and *Pleurodema*. The species of the *pentadactylus* group differ only slightly in that the foam-nest is deposited in pot holes filled with water along the edges of streams or ponds. The species in the *fuscus* or *sibilatrix* group deposit their eggs in a foam-nest in a burrow, and the tadpoles emerge after the nest is inundated. This recalls the situation seen in *Heleioporus*. The frogs of the *marmoratus* group deposit their few, large eggs in a terrestrial underground incubating chamber in a foam-nest. There are no aquatic larvae. *Edalorhina* has aquatic larvae (R. Etheridge, *in litt.*). Reproductive data are unavailable for *Barycholos*, *Hydrolaetare*, *Limnomedusa*, *Lithodytes*, and *Paratelmatobius*.

The subfamily Leptodactylinae was defined by Noble (1931) on the basis of the presence of an osseous style in the sternum. Other authors suggested that the foam-nest habits are characteristic of the subfamily, but these authors mistakenly believed that *Pseudopaludicola* is not related to the Leptodactylinae. In view of the appearance and variability of sternal styles and osseous plates elsewhere among the *Salientia*, it can be argued that the subfamily Leptodactylinae is poorly defined and possibly polyphyletic (see generic account for *Paratelmatobius*, pp. 182-4). Progressively graduated vicinal similarities of several characters within this group of genera were used to infer relationship through the whole set of genera.

The sternum is an osseous plate in *Paratelmatobius* with a large cartilaginous xiphisternum. In the other nine genera of the subfamily, the sternum is a style. In *Pleurodema* the style is relatively broad, and in *Limnomedusa*, *Barycholos*, *Edalorhina*, and *Physalaemus*, the style is only slightly narrower than that of *Pleurodema*. The sternal style is elongate and narrow in *Hydrolaetare*, *Leptodactylus*, *Lithodytes*, and *Pseudopaludicola*. I consider the presence of a discrete style in the sternum as sound evidence of close relationship. The relationships of *Paratelmatobius* are obscure —it does not have a bony style in the sternum. The transverse processes of the posterior presacral vertebrae are somewhat shortened in *Lithodytes*, *Paratelmatobius*, *Physalaemus*, *Pleurodema*, and *Pseudopaludicola*, but are not shortened in *Barycholos*, *Edalorhina*, *Hydrolaetare*, *Leptodactylus*, or *Limnomedusa*. The occipital condyles are relatively large and narrowly separated in *Limnomedusa* and *Pleurodema*. *Limnomedusa* has a type II cervical cotylar arrangement whereas, all other genera of the subfamily have a type I cervical cotylar arrangement.

I consider *Pleurodema* most like the primitive leptodactyline stock because it has a generalized body form, pectoral architecture, skeleton, and tadpole. *Pleurodema* is specialized in one interesting character—the loss of the quadratojugal. *Pleurodema* is externally similar to *Eupsophus*, and the external similarity reflects the similarity in the osteology of these two genera. The two genera are readily distinguished by the loss of the quadratojugal in *Pleurodema* and the presence of a bony style in the sternum of *Pleurodema*. The tadpole of *Pleurodema* has a median vent, 2/3 tooth rows, and a broad anterior interruption of the labial papillae, as do the tadpoles of *Eupsophus* and *Leptodactylus*. The tadpoles of *Physalaemus* and *Pseudopaludicola* have a dextral vent, 2/3 tooth rows, and a broad anterior interruption of the labial papillae. Noble (1931) suggested that *Physalaemus* was the stem genus of the Leptodactylinae, but my study suggests that *Pleurodema* more accurately fills this role. *Physalaemus* has departed from other leptodactylines in several morphological features, the most striking of which is the hyolaryngeal apparatus.

Pleurodema Tschudi, 1838
(Fig. 111)

Pleurodema Tschudi, 1838, Class. Batr., p. 47 [Type-species by monotypy, *Pleurodema bibroni* Tschudi, 1838].

Leiuperus Duméril and Bibron, 1841, Érpetologie généralé, 8:420 [Type-species by monotypy, *Leiuperus marmoratus* Duméril and Bibron, 1841].

Physalaemus Fitzinger (*non Physalaemus* Fitzinger, 1826), 1843, Syst. Rept., p. 31 [Type-species by original designation, *Cystignathus bibroni* of Duméril and Bibron, 1841 (=*Pleurodema bibroni* Tschudi, 1838)].

Lystris Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:312 [Type-species by monotypy, *Lystris brachyops* Cope, 1868].

Diagnostic definition.—1) sternum bearing a broad, osseous style which tends to bifurcate in large adult females; 3) transverse processes of posterior presacral vertebrae somewhat shortened; 4) cervical cotylar arrangement type I; 7) omosternum cartilaginous, usually not

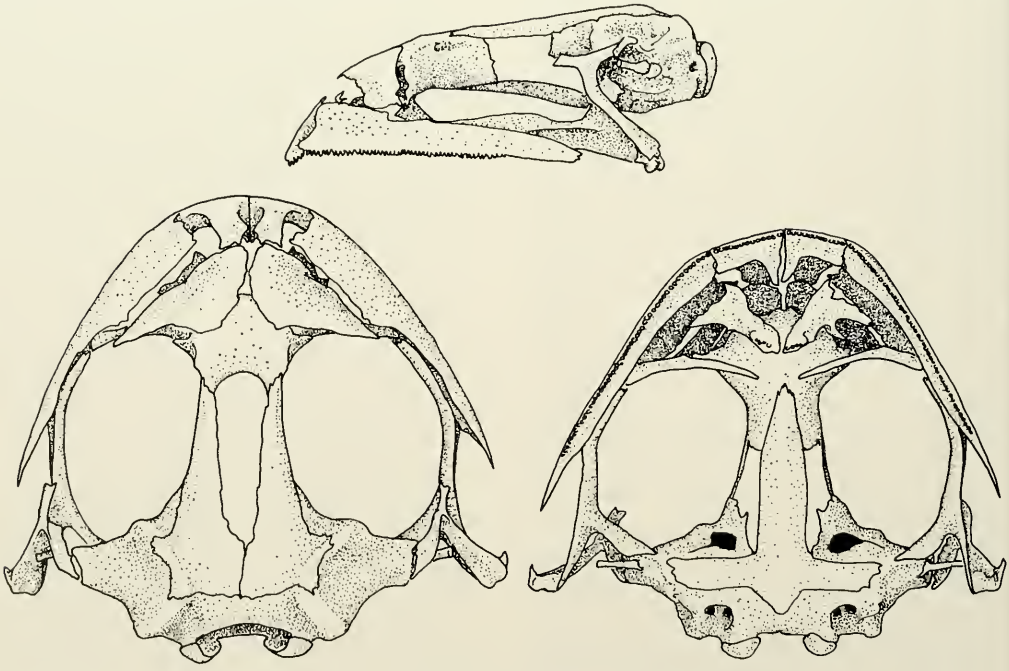

FIGURE 111. Lateral, dorsal, and ventral views of skull of *Pleurodema cinerea* (KU 80836, × 4).

elongated, manubrium large; 8) sacral diapophyses slightly dilated; 9) maxillary arch toothed; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla broad; 12) facial lobe of maxilla deep; 13) palatal shelf of maxilla narrow, pterygoid process lacking; 14) maxillary arch incomplete, quadratojugal lacking; 15) nasals in median contact, relatively small; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences small; 23) cristae paroticae relatively short, narrow; 24) zygomatic ramus of squamosal relatively short; 25) otic ramus of squamosal slightly longer than zygomatic ramus, no otic plate; 26) squamosal-maxillary angle 40-45°; 27) columellae present; 28) prevomers relatively large, toothed, narrowly separated medially; 29) palatines relatively narrow, arched, narrowly separated medially; 30) sphenethmoid large, extending anteriorly to posterior edge of nasals; 31) anterior ramus of parasphenoid long, narrow, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, broadly separated from median rami of pterygoids; 33) pterygoids relatively slender, anterior rami long, reaching palatines; 34) occipital condyles large, not stalked, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 41) pupil horizontal; 42) males with median subgular vocal sac, nuptial asperities on thumb; 43) lumbar glands present or not; 44) tongue large, round; 45) toes lacking webbing, with lateral fringes or not, metatarsal tubercles spade-like or not, digital tips narrow; 46) larvae with median vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 48) eggs laid in foam-nest in water, small and numerous; 49) adults 35-65 mm. SVL; 50) tympanum visible externally or concealed.

Composition.—Ten species are presently recognized: *bibroni, brachyops, bufonina, cinerea, darwinii, diplolistris, guayapae, marmorata, nebulosa,* and *tucumana.*[12] The widespread *P. bibroni* is probably a composite superspecies.

Distribution.—Central Andean Peru south to southern Chile and Argentina and northeastward to Uruguay, along the coastal lowlands of extreme eastern Brasil in non-forested habitats; the arid and semiarid coastal belt from the Guayanas through Venezuela to the Maricaibo Basin, the islands north of Venezuela, and in the savanas of central Panamá.

Remarks.—With the exception of *P. brachyops* and *P. diplolistris*, frogs of the genus *Pleurodema* are restricted to southern South America and temperate climates; *P. diplolistris* occurs in the subtropical areas of eastern Brasil, and *P. marmorata* ranges northward in the high Andes to central Peru. *Leiuperus verrucosus* Reinhardt and Lütken was placed in *Pleurodema* by Parker (1927), who was uncritically followed by all subsequent authors. The species is a member of the genus *Ischnocnema* (Telmatobiinae, Eleutherodactylini).

Parker (1927) included 18 nominal species in *Pleurodema.* Since his revision of the genus one new species *(guayapae)* has been named; *Pleurodema illota* is now placed in *Eupsophus,* and *P. mexicanus* is an *Eleutherodactylus.* Parker recognized *P. pseudophryne* Philippi and *P. montevidense* Philippi, which are now considered synonyms of *P. bibroni* and *P. darwinii,* respectively. Parker included *Pleurodema coquimbensis* in

[12] Donoso-Barros (1969) pointed out that *Pleurodema bibronii* Tschudi, 1838, is the same as *Pleurodema darwinii* Bell, 1843, and that the taxon Duméril and Bibron (1841) called *Pleurodema bibronii* is *Bufo thaul* Lesson, 1826. Thus *Pleurodema bibronii* Tschudi applies to the Uruguayan species called *P. darwinii,* and the correct name for the Chilean frogs called *P. bibronii* by most authors is *P. thaul* (Lesson), 1826.

Physalaemus, but Cei (1962a) pointed out that it is a synonym of *Pleurodema bibroni.*

At present, the most pressing systematic problem in the genus *Pleurodema* is the status of the species presently called *P. bibroni* and *P. cinerea.* Schmidt (1954b) recognized *P. plebeya* Philippi for the southern populations now called *P. bibroni.* Cei (1962a) combined the two nominal species but realized that the complex is seriously in need of further study. *Pleurodema cinerea* is closely related to *P. bibroni*; the two species are distinguished only by the external expression of the tympanum (concealed in *bibroni,* evident in *cinerea*). The *bibroni-cinerea* complex is much in need of a detailed review.

Of the ten species of *Pleurodema* recognized here, five *(bibroni, brachyops, bufonina, cinerea,* and *darwinii)* have lumbar or lumbo-inguinal glands. These glands are well-defined, often brightly patterned, and present in both sexes. At least some of these species use the glands in a defense posture. The frog arches its back and tucks its head down thus presenting the large, patterned glands to a predator or aggressor. In this position, the glands appear to be large eyes (Cei, 1962a). The lumbar glands are moderate-sized in *bibroni, brachyops, cinerea,* and *darwinii,* and very large in *bufonina.*

Parker (1927) suggested that the species of *Pleurodema* with prevomerine teeth were more primitive than those lacking prevomerine teeth. Like so many other herpetologists of the 19th and early 20th centuries, Parker (1927) regarded the presence or absence of prevomerine teeth as a major character in leptodactylid classification. His primary "key character" in subdividing the genus was the presence or absence of prevomerine (vomerine) teeth. As has been repeatedly pointed out in recent years, the prevomerine teeth are readily lost in many groups of frogs. The teeth may be present but concealed beneath the tissue of the palate (as in *Eleutherodactylus myersi*) or they may be lost entirely. In most of the cases where the presence of prevomerine teeth has been reported to be variable within a species, I have found that the teeth are present but concealed beneath the tissue of the palate. Main (1957) criticized the use of the presence of prevomerine teeth as the primary character in the division of the species of *Crinia* into two groups.

In four species of *Pleurodema (bibroni, bufonina, cinerea,* and *marmorata),* the metatarsal tubercles are not enlarged. In these species, the outer metatarsal tubercle is small and conical and the inner metatarsal tubercle is an elongate oval. In the other six species of the genus, the inner metatarsal tubercle is enlarged, laterally compressed, and spade-like. In these six species, the outer metatarsal tubercle is enlarged and either compressed *(brachyops, diplolistris, guayapae,* and *nebulosa)* or not *(darwinii* and *tucumana).*

Pleurodema bibroni and *cinerea* have a short inner tarsal fold, and *bufonina* has a long inner tarsal fold; all other species of the genus lack tarsal folds. *Pleurodema diplolistris* has a prominent tarsal tubercle, much like that seen in many species of *Physalaemus. Pleurodema nebulosa* has a fimbriated anal flap, whereas no other species of the genus has more than a low transverse ridge above the anal opening. The significance of these characters is not apparent at this time, although the presence of a tarsal fold in *bibroni, cinerea,* and *bufonina* is suggestive that they are closely related. These three species also agree in having lumbar glands and in having small, non-compressed metatarsal tubercles.

Of the eleven species listed in the genus *Pleurodema* by Gorham (1966), two are not included in this genus by me: *sagittifer* O. Schmidt, 1857, is here treated as a *species inquierenda,* and *verrucosus* Reinhardt and Lütken, 1862,

is placed in the genus *Ischnocnema* (Telmatobiinae, Eleutherodactylini).

Limnomedusa Fitzinger, 1843
(Fig. 112)

Limnomedusa Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, *Cystignathus macroglossus* Duméril and Bibron, 1841].

Litopleura Jiménez de la Espada, 1875, Vert. Viaje Pacif., Batr., p. 82 [Type-species by monotypy, *Litopleura maritimum* Jiménez de la Espada, 1875].

Diagnostic definition.—1) sternum bearing a broad osseous style; 3) transverse processes of posterior presacral vertebrae not shortened; 4) cervical cotylar arrangement type II; 7) omosternum cartilaginous, somewhat elongated, manubrium large; 8) sacral diapophyses round; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, broad at base; 11) palatal shelf of premaxilla relatively narrow; 12) facial lobe of maxilla moderately deep; 13) palatal shelf of maxilla narrow, pterygoid process small; 14) maxillary arch complete; 15) nasals relatively small, narrowly separated medially; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle large; 19) frontoparietals not ornamented; 22) epiotic eminences moderately large; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal short; 25) otic ramus of squamosal long, no otic plate; 26) squamosal-maxillary angle about 40°; 27) columellae present; 28) prevomers small, entire, toothed, widely separated medially; 29) palatines slender, widely separated medially; 30) sphenethmoid not reaching nasals; 31) anterior ramus of parasphenoid narrow, not keeled; 32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; 33) pterygoids small, all rami slender, anterior rami long, reaching palatines; 34) occipital condyles large, not stalked, narrowly separated medially; 36) terminal phalanges knobbed; 37) hyoid plate

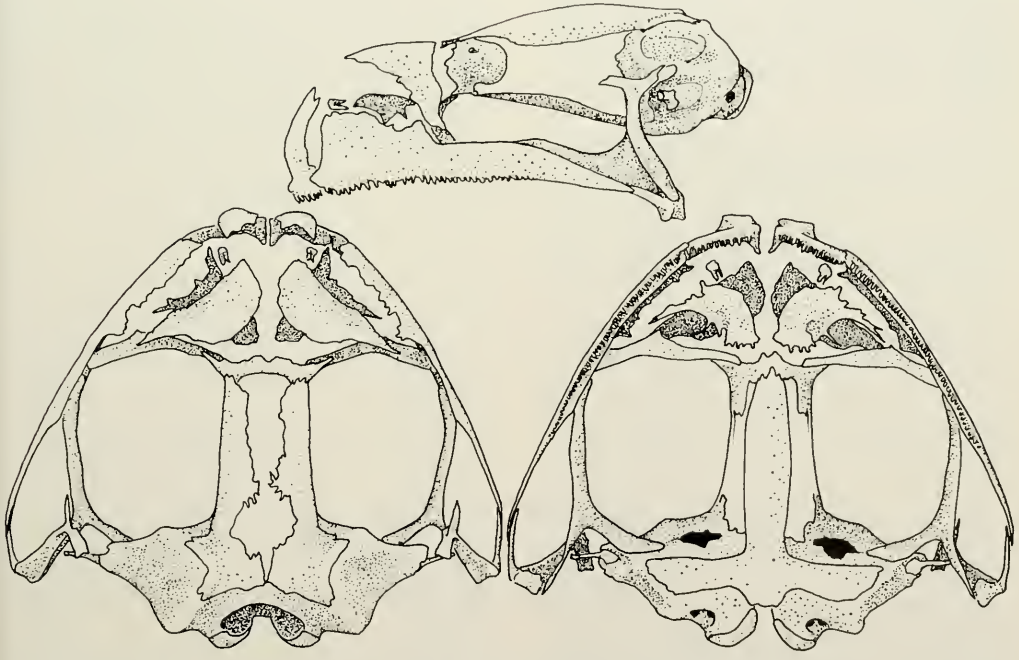

Figure 112. Skull of *Limnomedusa macroglossa*. Dorsal, ventral, and lateral views. (KU 92960, × 3.5).

lacking alary processes; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 41) pupil vertical; 42) males with median subgular vocal sac, nuptial asperities on thumb; 43) body free of glands; 44) tongue large, round; 45) toes fringed, basally webbed, metatarsal tubercles not enlarged, digital tips narrow; 46-48); 49) adults less than 60 mm. SVL; 50) tympanum visible externally.

Composition.—Two species are recognized: *macroglossa* and *misiones*.

Distribution.—Coastal lowlands of southern Brasil, Uruguay, and adjacent Misiones Province, Argentina. In Brasil, the genus is found in Paraná, Santa Catarina, and Rio Grande do Sul.

Remarks.—Frogs of this genus bear considerable external resemblance to *Leptodactylus* but differ from it in having vertical pupils, a nuptial pad on the thumb of the male, and a broad sternal style. *Limnomedusa* differs from all other leptodactylines in having a type II cervical cotylar arrangement.

Nothing is known of the breeding biology of the frogs of this genus. The presence of a nuptial pad on the thumb suggests that clasping takes place in water.

Hydrolaetare Gallardo, 1963
(Figs. 113-14)

Hydrolaetare Gallardo, 1963, Neotropica, 9:42 [Type-species by original designation, *Limnomedusa schmidti* Cochran and Goin, 1959].

Diagnostic definition.—1) sternum bearing an elongate osseous style; 3) transverse processes of posterior presacral vertebrae not shortened; 4) cervical cotylar arrangement type I: 7) omosternum large, elongate, cartilaginous; 8) sacral diapophyses rounded; 9) maxillary arch toothed; 10) alary processes of premaxillae directed posterodorsally, broad at base; 11) palatal shelf of premaxilla broad; 12) facial lobe of maxilla deep; 13) palatal shelf of maxilla moderately wide, no pterygoid process;

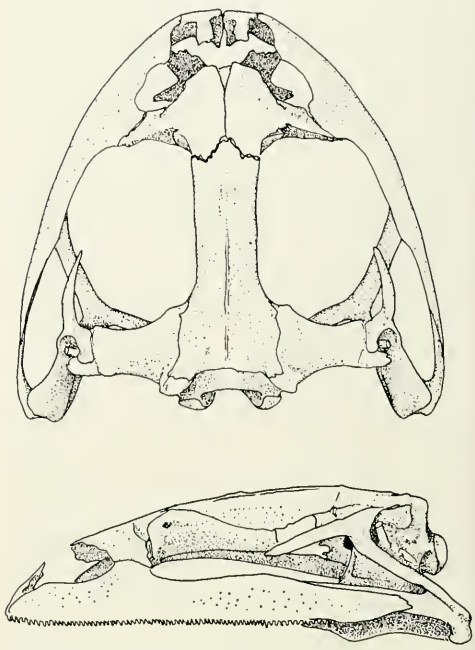

FIGURE 113. Dorsal and lateral views of skull of *Hydrolaetare schmidti* (KU 110613, × 3).

14) maxillary arch complete; 15) nasals relatively large, in broad median contact; 16) nasals in broad contact with maxillae, separated from pterygoids; 17) nasals in broad contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietal bearing sagittal crest, slight exostosis; 22) epiotic eminences large posteriorly; 23) cristae

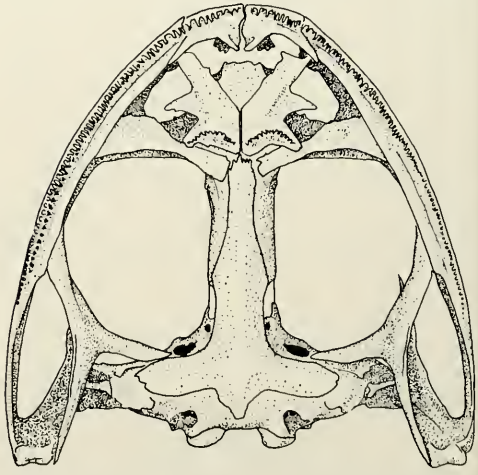

FIGURE 114. Ventral view of skull of *Hydrolaetare schmidti* (KU 110613, × 3).

paroticae narrow, relatively short; 24) zygomatic ramus of squamosal elongate; 25) otic ramus of squamosal relatively short, expanded medially into small otic plate; 26) squamosal-maxillary angle about 30°; 27) columella present; 28) prevomers large, toothed, in median contact; 29) palatines broad, separated medially by anterior ramus of parasphenoid, bearing odontoid ridge; 30) sphenethmoid extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid narrow anteriorly, extending to between palatines, not keeled medially; 32) parasphenoid alae deflected posteriorly, broadly overlapped by median rami of pterygoids; 33) pterygoids large, anterior rami extending to middle of orbit, prominent ventral flange present; 34) occipital condyles of moderate size, not stalked, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate wing-like; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 41) pupil vertical; 42) males with median subgular vocal sac, no nuptial asperities; 43) body lacking glands; 44) tongue large, deeply notched posteriorly; 45) toes fully webbed, metatarsal tubercles not enlarged, digital tips narrow; 46-48); 49) adults large, known specimens 80-105 mm. SVL; 50) tympanum visible externally.

Composition.—Monotypic.

Distribution.—Amazonian South America.

Remarks.—Cochran and Goin (1959) named *Limnomedusa schmidti* on the basis of a single specimen collected near Leticia, Colombia. They pointed out that the new species was strikingly different from the other two species of *Limnomedusa.* Gallardo (1963) reported additional specimens of the species and named a new genus for it *(Hydrolaetare).* *Hydrolaetare* and *Limnomedusa* share only two significant characters—vertical pupils and an osseous element in the sternum.

Several osteological characters of *Hydrolaetare* suggest that the genus is allied to the Grypiscini (Telmatobiinae). As in *Cycloramphus* and *Zachaenus, Hydrolaetare* has a relatively deep maxilla and quadratojugal, the nasals are relatively large, in broad median contact, and in broad contact with the maxillae, the nasals are in broad contact with the frontoparietals, the skull lacks a fontanelle and has a sagittal crest, the zygomatic ramus of the squamosal is elongate, and the pterygoid bears a ventral flange. Unfortunately, reproductive data are lacking for *Hydrolaetare,* but the species lacks nuptial pads on the thumb, suggesting that amplexus occurs in terrestrial situations (as in the Grypiscini). The three genera now included in the Grypiscini have large, cartilaginous sterna, in contrast to the leptodactyline sternum of *Hydrolaetare.* On the basis of the skull alone, I would place *Hydrolaetare* in the Grypiscini, but the sternal apparatus and striking similarity between *Hydrolaetare* and *Leptodactylus* (*ocellatus* and *pentadactylus* groups) suggest that the genus is a leptodactyline. *Hydrolaetare* lacks one important character of the Grypiscini; the otic ramus of the squamosal of *Hydrolaetare* is not medially curved to form a broad otic plate. The otic plate of *Hydrolaetare* is small and like that seen in the *melanonotus, ocellatus,* and *pentadactylus* groups of *Leptodactylus.*

Edalorhina Jiménez de la Espada, 1870
(Fig. 115)

Edalorhina Jiménez de la Espada, 1870, J. Sci. Math. Phys. Nat., Lisboa, 3:58 [Type-species by monotypy, *Edalorhina perezi* Jiménez de la Espada, 1870].

Bubonias Cope, 1874, Proc. Acad. Nat. Sci. Philadelphia, 26:124 [Type-species by monotypy, *Bubonias plicifrons* Cope, 1874].

Diagnostic definition.—1) sternum bearing broad osseous style; 3) transverse processes of posterior presacral vertebrae not shortened; 4) cervical cotylar arrangement type I; 7) omosternum elongate, cartilaginous, manubrium large; 8) sacral diapophyses rounded;

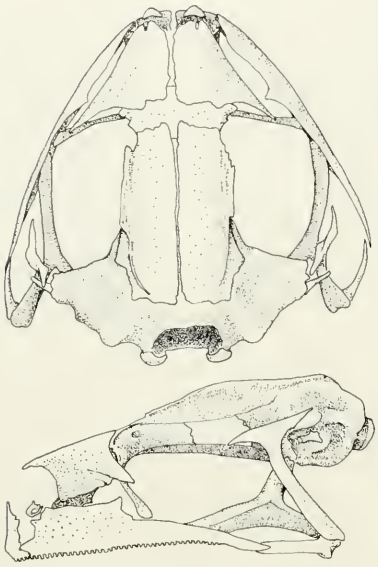

FIGURE 115. Dorsal and lateral views of skull of *Edalorhina perezi* (KU 124225, × 6.4).

9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, moderately wide at base; 11) palatal shelf of premaxilla of moderate width; 12) facial lobe of maxilla deep; 13) palatal shelf of maxilla relatively narrow, pterygoid process small; 14) maxillary arch complete; 15) nasals large, in broad median contact; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals bear large, exostosed, lateral crests; 22) epiotic eminences obsolete; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal of moderate length; 25) otic ramus of squamosal as long as zygomatic ramus, no otic plate; 26) squamosal-maxillary angle about 50°; 27) columella present; 28) prevomers relatively small, entire, toothed, separated medially, dentigerous processes lie posterior to choanae; 29) palatines slender, separated medially; 30) sphenethmoid short, extending anteriorly to posterior edge of nasals; 31) anterior ramus of parasphenoid broad, relatively short, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, narrowly overlapped laterally by median rami of pterygoids; 33) pterygoids slender, anterior rami long, nearly reaching palatines; 34) occipital condyles small, not stalked, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 41) pupil horizontal; 42) males with median subgular vocal sac, nuptial asperities on thumb; 43) inguinal glands present; 44) tongue large; 45) toes lacking webbing, metatarsal tubercles not enlarged, digital tips narrow; 46-48) larvae aquatic; 49) adults small, less than 45 mm. SVL; 50) tympanum visible externally.

Composition.—Two species are currently recognized: *nasuta* and *perezi*.

Distribution.—Amazonian lowlands of Ecuador and northern and central Peru, and in extreme western Brasil.

Remarks.—The genus was reviewed by Dunn (1949), who combined the nominal species *buckleyi*, *perezi*, and *plicifrons*, but noted that the Peruvian population of *perezi* usually lacks a snout projection, whereas the Ecuadorian population has one. Dunn also pointed out that Shreve's (1941) *Edalorhina pustulata* (Pacific lowlands of Ecuador) was not an *Edalorhina* but is closely related to the Middle American *Engystomops pustulosus*. I concur with Dunn but include *Engystomops* in *Physalaemus*.

Parker (1927) and Noble (1931) considered *Edalorhina* to be merely a *Physalaemus* with cranial crests and elongate papillae on the eyelids. Dunn (1949) disagreed and suggested that *Edalorhina* was more closely related to *Pleurodema*. I consider the genus to be intermediate between *Lithodytes* and *Physalaemus*. The breeding biology of *Edalorhina* is unknown and could provide useful clues to the relationships of the genus to the paludicoline leptodactylids.

Lithodytes Fitzinger, 1843
(Figs. 116-17)

Lithodytes Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, *Rana lineata* Schneider, 1799].

Diagnostic definition.—1) sternum bearing an elongate osseous style; 3) transverse processes of posterior presacral vertebrae somewhat shortened; 4) cervical cotylar arrangement type I; 7) omosternum bearing an elongate osseous style and large cartilaginous manubrium; 8) sacral diapophyses rounded; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, broad at base; 11) palatal shelf of premaxilla relatively broad; 12) facial lobe of maxilla relatively deep, not exostosed; 13) palatal shelf of maxilla relatively broad, no pterygoid process; 14) maxillary arch complete; 15) nasals large, in tenuous median contact; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals not ornamented; 22) epiotic eminences small; 23) cristae paroticae broad, stocky; 24) zygomatic ramus of squamosal relatively long; 25) otic ramus of squamosal short, expanded medially into small otic plate; 26) squamosal-maxillary angle about 50°; 27) columella present; 28) prevomers large, entire, toothed, narrowly separated medially; 29) palatines relatively narrow, widely separated medially; 30) sphenethmoid extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid broad, relatively short, not keeled medially; 32) parasphenoid alae deflected posteriorly, short, not overlapped laterally by median rami of pterygoids; 33) pterygoids slender, anterior rami long, not reaching palatines; 34) occipital condyles small, not stalked, widely separated medially; 36) terminal phalanges T-shaped; 37) alary processes of hyoid plate on narrow stalks; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 41) pupil horizontal; 42) male with median subgular vocal sac, no nuptial asperities; 43) body lacking glands; 44) tongue large, rounded; 45) toes lacking webbing, metatarsal tubercles not enlarged, digital tips dilated, each pad bearing terminal transverse groove; 46-48); 49) adults medium-sized, to 50 mm. SVL; 50) tympanum visible externally.

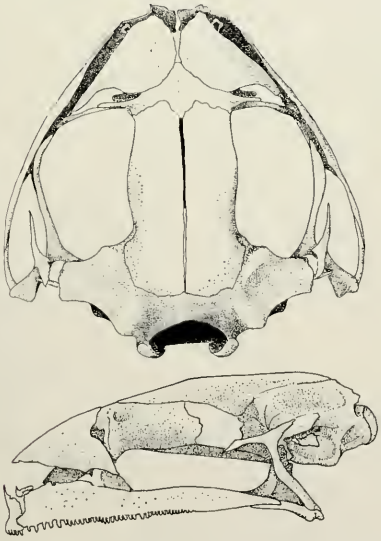

FIGURE 116. Dorsal and lateral views of skull of *Lithodytes lineatus* (KU 104340, × 2.6).

FIGURE 117. Ventral view of skull of *Lithodytes lineatus* (KU 104340, × 2.6).

Composition.—Monotypic.

Distribution.—Edge of the Amazon Basin from Guayana to Bolivia.

Remarks.—Several authors have placed *Lithodytes lineatus* in *Eleutherodactylus*. Some did so following Noble (1917), who ignored the presence of

osseous styles in the omosternum and sternum and placed extra weight on the presence of T-shaped terminal phalanges. Ruthven (1919) effectively rejected Noble's arguments.

Rana lineata Schneider has been frequently confused with *Hylodes lineatus* Brocchi. The latter is a Guatemalan species of *Eleutherodactylus* and bears no resemblance to the Amazonian *Lithodytes lineatus. Lithodytes lineatus* bears considerable superficial resemblance to some species of the *Eleutherodactylus fitzingeri* group. Dunn (1931) named *Lithodytes gaigeae* (erroneously spelled *gaigei*), a species found in Costa Rica and Panamá, and Piatt (1934) correctly pointed out that *gaigeae* was a species of *Eleutherodactylus.* The two species are strikingly similar in color pattern.

The skull of *Lithodytes* bears considerable resemblance to those of the paludicoline genera, but the sternal style is elongate, like that of *Leptodactylus.* The hyolaryngeal apparatus of *Lithodytes* is like that seen in *Edalorhina, Leptodactylus,* and *Pleurodema.* Nothing is known of the breeding biology of *Lithodytes,* but the lack of nuptial asperities suggests that the genus clasps on land and may exhibit direct development like the species of the *Leptodactylus marmoratus* group.

Physalaemus Fitzinger, 1826
(Figs. 118-19)

Physalaemus Fitzinger, 1826, Neue Class. Rept., p. 39 [Type-species by monotypy, *Physalaemus cuvieri* Fitzinger, 1826].

Paludicola Wagler, 1830, Syst. Amph., p. 206 [Type-species by monotypy, *Bufo albifrons* Spiz, 1824].

Gomphobates Reinhardt and Lütken, 1862, Vid. Meddel. Naturh. Foren., 1861:172 [Type-species by monotypy, *Gomphobates notatus* Reinhardt and Lütken, 1862].

Eupemphix Steindachner, 1863, Sber. Akad. Wiss. Wien, 48:188 [Type-species by monotypy, *Eupemphix nattereri* Steindachner, 1863].

Nattereria Steindachner, 1864, Verh. Zool.-Bot. Ges. Wien, 1864:279 [Type-species by monotypy, *Nattereria lateristrigata* Steindachner, 1864].

Iliobates Fitzinger *in* Steindachner, 1867, Reise Novara, p. 12 [Listed as a generic synonym (manuscript name) of *Gomphobates fuscomaculatus* Steindachner; this generic name is invalid and not available].

Engystomops Jiménez de la Espada, 1872, An. Soc. Española Hist. Nat., 1:86 [Type-species by monotypy, *Engystomops petersi* Jiménez de la Espada, 1872].

Microphryne W. Peters, 1873, Mtber. k. Preuss. Akad. Wiss. Berlin, 1873:616 [Type-species by monotypy, *Paludicola (Microphryne) pustulosa* Cope, 1864].

Peralaimos Jiménez de la Espada, 1875, Vert. Viaje Pacif. Batr., p. 163 [Type-species by monotypy, *Bufo stentor* Jiménez de la Espada, 1872].

Diagnostic definition.—1) sternum bearing relatively broad osseous sternal style; 3) transverse processes of posterior presacral vertebrae somewhat shortened; 4) cervical cotylar arrangement type I; 7) omosternum elongate, cartilaginous, manubrium small to large; 8) sacral diapophyses slightly dilated; 9) maxillary arch toothed or not; 10) alary processes of premaxillae directed dorsally or slightly anterodorsally, relatively narrow at base; 11) palatal shelf of premaxilla relatively broad; 12) facial lobe of maxilla short, of moderate depth; 13) palatal shelf of maxilla narrow, no pterygoid process; 14) maxillary arch complete; 15) nasals relatively large, in broad median contact; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals not ornamented; 22) epiotic eminences small; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal short; 25) otic ramus of squamosal short, no otic plate; 26) squamosal-maxillary angle about 60°; 27) columella present; 28) prevomers entire, small, usually toothless, widely separated medially; 29) palatines long, slender, widely separated medially; 30) sphenethmoid extending anteriorly beneath posterior part of nasals; 31) anterior ramus of parasphenoid narrow, not keeled medially; 32) parasphenoid alae oriented at right angles to anterior ramus, narrowly separated from or narrowly over-

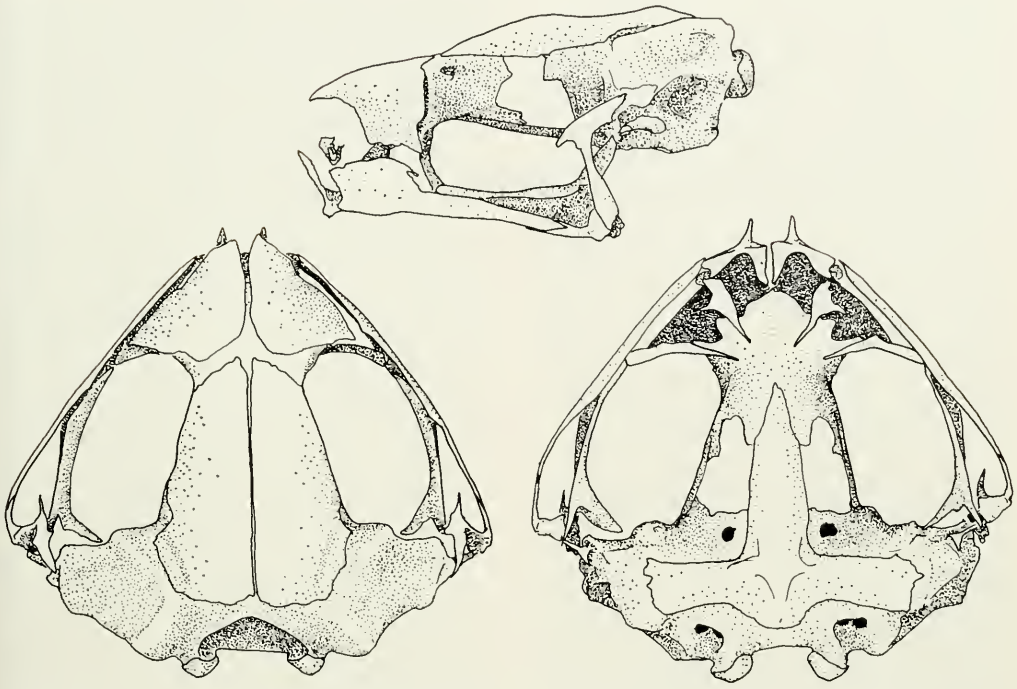

FIGURE 118. Lateral, dorsal, and ventral views of skull of *Physalaemus pustulosus* (KU 68271, × 4.7).

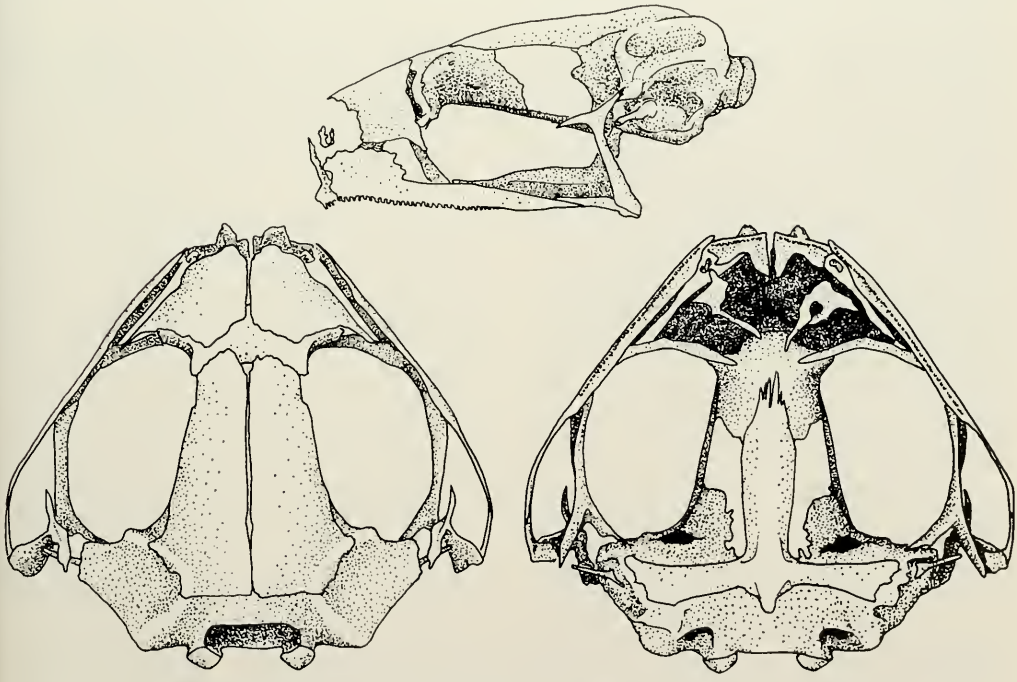

FIGURE 119. Lateral, dorsal, and ventral views of skull of *Physalaemus ephippifer* (KU 93005, × 4.7).

lapped laterally by median rami of pterygoids; 33) pterygoids slender, rami long, anterior rami reaching palatines; 34) occipital condyles small, on short stalks, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate broad and wing-like; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on hyoid plate near midline; 41) pupil horizontal; 42) males with large external subgular vocal sacs, tending to bilobe, males with nuptial pads on thumb; 43) parotoid glands present or absent, inguinal glands present or absent, flank glands present or absent; 44) tongue relatively narrow; 45) toes free of webbing and lateral fringes, tarsus bearing tubercle on inner edge or not, metatarsal tubercles enlarged and spade-like or not, digital tips narrow; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 48) eggs small, numerous, laid in foam nest floating on water; 49) adults range in size from 17-60 mm. SVL; 50) tympanum usually concealed, visible externally in *pustulatus*.

Composition.—With the combination of the nominal genera *Engystomops, Eupemphix,* and *Physalaemus* into a single genus, *Physalaemus* is one of the larger genera of leptodactylids. I recognize 34 nominal species *(aguirrei, albifrons, albonotatus, barrioi, biligonigerus, centralis, cicada, cuvieri, enesefae, ephippifer, evangelistai, fernandezae, fuscomaculatus, gracilis, henseli, kroeyeri, jordanensis, maculiventris, moreirae, nanus, nattereri, obtectus, olfersi, paraensis, petersi, pustulatus, pustulosus, riograndensis, santafecinus, schereri, signiferus, soaresi, stentor,* and *ternetzi).*

Distribution.—Southern México to Argentina in lowland non-forested regions (and through second growth and occasionally primary forest) except for the very arid Pacific lowlands south of Ecuador and over most of central and southern Argentina and Chile.

Remarks.—In a separate paper, I (Lynch, 1970b) justified the combination of *Engystomops, Eupemphix,* and *Physalaemus.* In that paper I suggested the recognition of at least four species groups—the *petersi* group, the *maculiventris* group, the *curvieri* group, and the *fuscomaculatus* group.

Physalaemus has the criniine pattern of insertion of the hyoid musculature on the hyoid plate. The only other Neotropical leptodactylids with this pattern are the species of the *Leptodactylus marmoratus* group and the genus *Pseudopaludicola,* although the hyoid plate of *Hydrolaetare* is like that seen in *Physalaemus* and *Pseudopaludicola.* For the present I consider *Physalaemus* and *Pseudopaludicola* to be relatively closely related but realize that the two genera differ in many respects. In some characteristics *Physalaemus* is closest to *Leptodactylus* and *Pleurodema,* but in others it is closer to *Edalorhina, Lithodytes,* and *Paratelmatobius.*

Paratelmatobius B. Lutz and Carvalho, 1958

(Fig. 120)

Paratelmatobius B. Lutz and Carvalho, 1958, Mem. Inst. Oswaldo Cruz, 56:241 [Type-species by original designation, *Paratelmatobius lutzi* B. Lutz and Carvalho, 1958].

Diagnostic definition.—1) sternum bearing a broad osseous plate; 3) transverse processes of posterior presacral vertebrae shortened; 4) cervical cotylar arrangement type I; 7) omosternum present, small, cartilaginous, manubrium minute; 8) sacral diapophyses dilated; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, narrow at base; 11) palatal shelf of premaxilla broad; 12) facial lobe of maxilla shallow, expanded in snout region; 13) palatal shelf of maxilla broad, pterygoid process moderate-sized; 14) maxillary arch complete; 15) nasals small, narrow, separated medially; 16) nasals not contacting maxillae or pterygoids, nasal with elongate maxillary process which nearly reaches maxilla; 17) nasals

not in contact with frontoparietals; 18) frontoparietal fontanelle moderate-sized; 19) frontoparietals not ornamented; 22) epiotic eminences well defined; 23) cristae paroticae short, stocky; 24) zygomatic ramus of squamosal relatively long, slender; 25) otic ramus of squamosal short, curved medially to form small otic plate; 26) squamosal-maxillary angle about 55°; 27) columella absent; 28) prevomers small, entire, toothed, widely separated medially; 29) palatines thin, elongate, broadly separated medially; 30) sphenethmoid extending anteriorly to middle of nasals; 31) anterior ramus of parasphenoid broad, short, lacking median keel; 32) parasphenoid alae short, narrow, deflected posteriorly, not overlapped laterally by median rami of pterygoids; 33) pterygoids small, median rami short, anterior rami not reaching palatines; 34) occipital condyles large, not stalked, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate on narrow stalks; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edge of hyoid plate; 41) pupil horizontal; 42) males lacking vocal sac, nuptial pads on first two fingers; 43) body lacking glands; 44) tongue large, round; 45) toes fully webbed, metatarsal tubercles not enlarged, digital tips narrow; 46-48); 49) adults small, less than 30 mm. SVL; 50) tympanum concealed.

Composition.—Two species are presently known *(lutzi* and *gaigeae).* The latter was named *P. pictiventris* A. Lutz in B. Lutz and Carvalho (1958) but is a *nomen nudum* and an obligate synonym of *Leptodactylus gaigeae* Cochran, 1938.

Distribution.—The coastal ranges in Estado Rio de Janeiro, Brasil.

Remarks.—Aldopho Lutz collected the first specimens of this genus in December 1931. He made water color sketches of the two specimens and noted that they represented a new species of *Paludicola* or *Eupemphix.* However, he never described the specimens or otherwise published on them. Cochran (1938) who received these two specimens, named and described them as

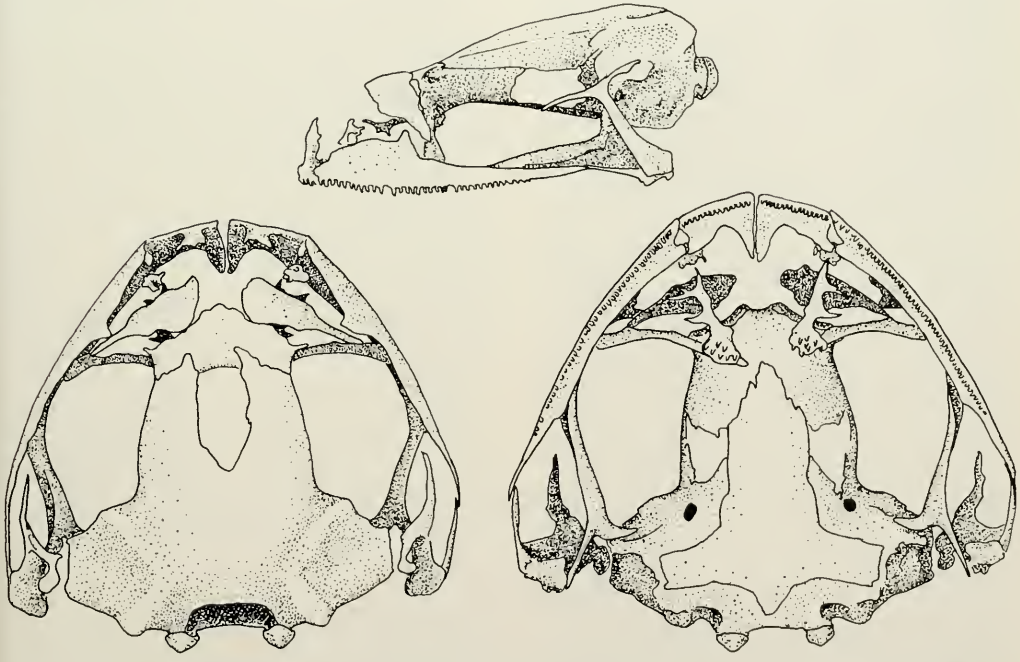

FIGURE 120. Lateral and dorsal (KU 107089) and ventral (KU 92981) views of skulls of *Paratelmatobius lutzi.* All × 8.

Leptodactylus gaigeae. She suggested that the species was related to *L. marmoratus* and served as a generic link between *Leptodactylus* and *Zachaenus.* Lutz and Carvalho (1958) discovered a new species allied to the frogs collected by A. Lutz nearly 30 years before and named it as a new genus and new species, *Paratelmatobius lutzi*; at the same time they published A. Lutz's figures of the other species and used his manuscript name, *P. pictiventris,* for them. They suggested that *Paratelmatobius* was intermediate between the endemic southeastern Brasilian genus *Cycloramphus* and the Andean *Telmatobius.*

The architecture of the otic ramus of the squamosal of *Paratelmatobius* is identical to that seen in the Grypiscini, and the four genera bear considerable external resemblance to one another. The sternal plate in *Paratelmatobius* is not like the sternal style seen in the leptodactylines but appears to be an ossification of the sternal plate—an advancement over the calcification of the same element seen in old individuals of a variety of leptodactylid genera and species. Nevertheless, *Paratelmatobius* differs in several osteological characters from the Grypiscini—the presence of a frontoparietal fontanelle, the wide median separation of the nasals, the absence of a ventral flange on the pterygoid.

In summary, *Paratelmatobius* is osteologically intermediate between the Leptodactylinae and the Grypiscini (Telmatobiinae). This might be regarded as some evidence for polyphyly of the Telmatobiinae since one group of Telmatobiinae (i.e., Alsodini) undoubtedly gave rise to the Leptodactylinae and I am here pointing out the possibility of genetic relationship between *Paratelmatobius* and the Grypiscini. The squamosal architecture of *Paratelmatobius* and the Grypiscini may be a parallel (or convergent) development rather than a result of relationship. The appearance of a very similar otic plate in *Megaelosia* (Elosiinae) is very suggestive that the appearance of this sort of otic ramus is a labile feature and should not be used in primary inferences of relationships. In the Grypiscini, several other osteological characters combine to render this character confirmatory and therefore it is used in the diagnosis of that group (p. 135). I am tentatively assigning *Paratelmatobius* to the Leptodactylinae. In several respects the genus bears some similarity to *Physalaemus,* although I do not regard the relationship (if any) to be close.

The presence of nuptial asperities and a frontoparietal fontanelle, although small, in *Paratelmatobius* suggest that the genus is not allied with the Eleutherodactylini. The nature of the occipital condylar-cervical articulation as well as a variety of other osteological and external characters does not permit its association with the Ceratophryinae, Alsodini, Odontophrynini or Telmatobiini. The Elosiinae is a compact group, and the external and many internal features serve to illustrate the lack of correspondence between *Paratelmatobius* and the Elosiinae. If a new family group is not proposed for this small genus, then the genus must belong to the Grypiscini or the Leptodactylinae. I have fewer difficulties associating it with the latter, perhaps because the latter is a more heterogeneous group. The presence of an osseous plate in the sternum, although it is rather unlike the sternal style seen in the other genera of the subfamily, is not contrary to the diagnostic feature of the subfamily. No other leptodactylid known to me normally possesses an osseous post-zonal element. Although the presence of an osseous post-zonal sternal element is the only uniform character in the subfamily, I consider the subfamily to be monophyletic (see the generic account of *Hydrolaetare* for further comment).

Pseudopaludicola Miranda-Ribeiro, 1926
(Fig. 121)

Pseudopaludicola Miranda-Ribeiro, 1926, Arch. Mus. Nac. Rio de Janeiro, 27:152 [Type-

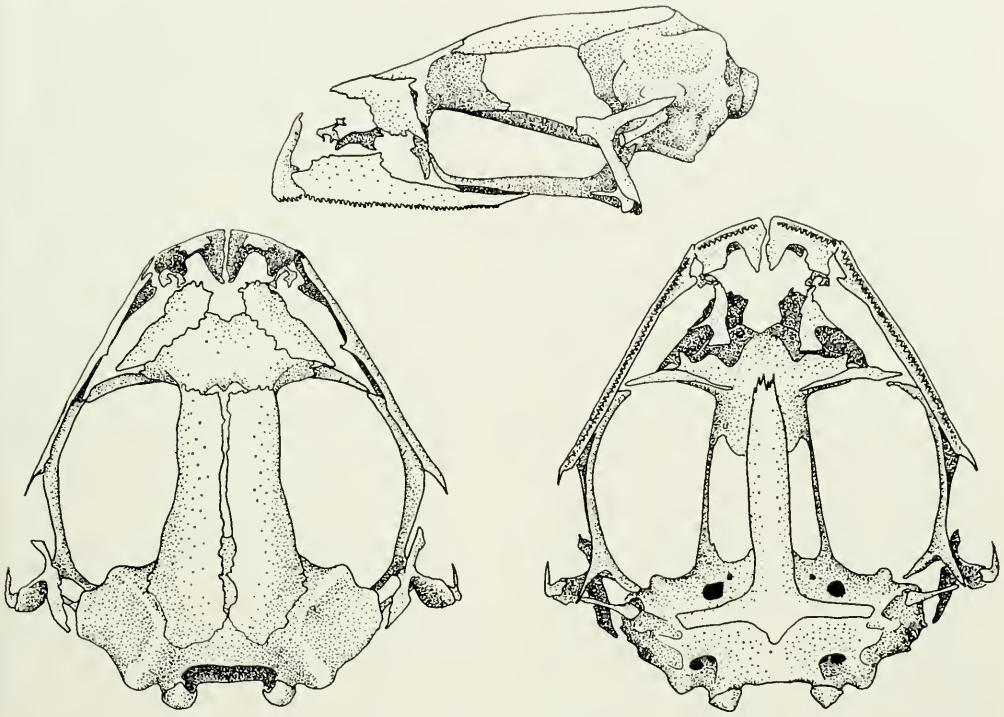

FIGURE 121. Lateral, dorsal, and ventral views of skull of *Pseudopaludicola falcipes* (KU 93068, × 8).

species by monotypy, *Liuperus (sic) falcipes* Hensel, 1867].

Diagnostic definition.—1) sternum bearing an elongate, osseous or calcified style; 3) transverse processes of posterior presacral vertebrae shortened; 4) cervical cotylar arrangement type I; 7) omosternum elongate, cartilaginous, manubrium small; 8) sacral diapophyses rounded; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, broad at base; 11) palatal shelf of premaxilla broad; 12) facial lobe of maxilla shallow; 13) palatal shelf of maxilla narrow, no pterygoid process; 14) maxillary arch incomplete, quadratojugal absent; 15) nasals small, widely separated medially; 16) nasals not in contact with maxillae or pterygoids; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle absent, frontoparietals usually narrowly separated for entire length; 19) frontoparietals not ornamented; 22) epiotic eminences obsolete; 23) cristae paroticae very short, broad; 24) zygomatic ramus of squamosal relatively short; 25) otic ramus of squamosal long, expanded medially into narrow otic plate; 26) squamosal-maxillary angle 50-60°; 27) columella present; 28) prevomers small, reduced to sliver-like elements, dentigerous rami lost, widely separated medially; 29) palatines narrow, sliver-like, in contact with maxillae, widely separated medially; 30) sphenethmoid very short, extending anteriorly to posterior edge of nasals; 31) anterior ramus of parasphenoid narrow, not reaching palatines, not keeled medially; 32) parasphenoid alae long, oriented at right angles to anterior ramus of parasphenoid, narrowly separated from median rami of pterygoids; 33) pterygoids small, median and posterior rami minute, anterior rami long, reaching to palatines; 34) occipital condyles small, stalked, widely separated medially; 36) terminal phalanges knobbed; 37) alary processes of hyoid plate wing-like; 39) *m. petrohyoideus*

anterior and *m. sternohyoideus* insert on hyoid plate near midline; 41) pupil horizontal; 42) males with bilobed subgular vocal sac, nuptial asperities lacking; 43) body lacking glands; 44) tongue large, oval; 45) toes lacking webbing and lateral fringes, metatarsal tubercles not enlarged, digital tips narrow; 46) larvae with dextral vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 48) eggs small, numerous, laid singly or in small clumps attached to submerged vegetation; 49) males reach 16 mm., females reach 19 mm. SVL; 50) tympanum concealed; 51) the antebrachial tubercles are generically unique.

Composition.—Parker (1927) recognized five species of the genus *(ameghini, boliviana, falcipes, pusilla,* and *saltica).* Bokermann (1966) recognized five species in the coastal lowlands of eastern and southern Brasil *(ameghini, falcipes, mystacalis, saltica,* and *ternetzi),* which Milstead (1963) had pronounced identical. I consider *boliviana* and *pusilla* to be conspecific (see "Remarks") and recognize six species *(ameghini, falcipes, mystacalis, pusilla, saltica,* and *ternetzi).*

Distribution.—The coastal lowlands of Brasil from Bahía to northeastern Argentina; Amazonian Bolivia, Paraguay, and Venezuela, and in the coastal ranges of Venezuela and the Santa Marta mountains of Colombia.

Remarks.—The genus *Pseudopaludicola* gained wide acceptance through the work of Parker (1927) and Barrio (1954). Parker included five species in the genus and considered two of these *(boliviana* and *pusilla)* to have T-shaped terminal phalanges. All species of the genus have elongate, knobbed terminal phalanges and agree in all details of skull ossification. Parker incorrectly characterized the genus as having a cartilaginous sternum (see account of pectoral girdles, pp. 58-60) and has been followed by all subsequent authors. I include the genus in the Leptodactylinae and consider it closely related to the paludicoline genera in spite of the ethological differences pointed out by Barrio (1954). The structure of the hyolarynx of *Pseudopaludicola* is not greatly different from that of *Physalaemus* but very different from that of all other Neotropical leptodactylids except *Hydrolaetare* and the *Leptodactylus marmoratus* group.

The species of this genus are readily distinguished from all other small leptodactylid frogs by their slender habitus, lack of digital webbing, unexpanded digital tips, concealed tympanum, and the presence of an antebrachial tubercle. The skeletons of the five nominal species available to me are indistinguishable.

Parker separated *boliviana* and *pusilla* on slight differences in leg length and coloration. I tentatively consider the two nominal species identical because I am unable to separate paratypes and topotypic material of each from one another. Rivero (1961) reported "*pusilla*" from Amazonian Venezuela and Parker (1935) reported "*boliviana*" from British Guiana and Paraguay. In view of the ethological differences recently discovered between the Brasilian species (W. C. A. Bokermann, pers. comm.), it might prove premature to combine the cis-Andean populations of *Pseudopaludicola* as a single species. The specimens examined by me represent a single morphological species. The Brasilian species were pronounced conspecific by Milstead (1963). Bokermann has since examined most of the types of this genus and is familiar with all of the Brasilian species in the field; he informs me that most of the previously named kinds represent valid species, and there are yet undescribed species living in the coastal lowlands of southeastern Brasil. All of the Brasilian species can be separated on the basis of call, leg length, and color pattern.

Leptodactylus Fitzinger, 1826

(Figs. 122-24)

Leptodactylus Fitzinger, 1826, Neue Class. Rept., p. 38 [Type-species by subsequent

designation, (Fitzinger, 1843), *Leptodactylus typhonia* (=*Rana typhonia* Daudin, 1803, *non Rana typhonia* Linné, 1758). *Rana typhonia* Daudin is *R. sibilatrix* Wied, 1824, which Heyer (1968) considered identical with *Rana fusca* Schneider, 1799, for which he designated a neotype. However, at least some of the syntypes of *Rana fusca* are extant (W. C. A. Bokermann, pers. comm.), and study of these must be made before Heyer's action can be accepted].

Cystignathus Wagler, 1830, Syst. Amph., p. 202 [Type-species by present designation, *Rana mystacea* Spix, 1824].

Gnathophysa Fitzinger, 1843, Syst. Rept., p. 31 [Type-species by original designation, *Rana labyrinthica* Spix, 1824].

Sibilatrix Fitzinger, 1843, *Ibid.*, p. 31 [Type-species by original designation, *Cystignathus gracilis* Duméril and Bibron, 1841].

Plectromantis W. Peters, 1862, Mtber. k. Preuss. Akad. Wiss. Berlin, 1862:232 [Type-species by monotypy, *Plectromantis wagneri* W. Peters, 1862].

Adenomera Steindachner, 1867, Reise Novara, Zool. Amph., p. 37 [Type-species by monotypy, *Adenomera marmorata* Steindachner, 1867].

Entomoglossus W. Peters, 1870, Mtber. k. Preuss. Akad. Wiss. Berlin, 1870:647 [Type-species by monotypy, *Entomoglossus pustulatus* W. Peters, 1870].

Pachypus A. Lutz, 1930, Mem. Inst. Oswaldo Cruz, 23:22 [Proposed as a subgeneric name of *Leptodactylus*; no type-species was designated. Preoccupied by *Pachypus* Billberg, 1820 (Insecta: Coleoptera), *Pachypus* d'Alton, 1840 (Mammalia), and *Pachypus* Cambridge, 1873 (Arachnida)].

Cavicola A. Lutz, 1930, *Ibid.*, 23:22 [Proposed as a subgeneric name of *Leptodactylus*; no type-species was designated. Preoccupied by *Cavicola* Ancey, 1887 (Mollusca)].

Parvulus A. Lutz, 1930, *Ibid.*, 23:22 [Proposed as a subgeneric name in *Leptodactylus*; type-species by subsequent designation (Parker, 1932:342), *Leptodactylus nanus* L. Müller, 1922].

Diagnostic definition.—1) sternum bearing an elongate osseous style; 3) transverse processes of posterior presacral vertebrae not shortened; 4) cervical cotylar arrangement type I; 7) omosternum large, elongate, cartilaginous, manubrium large; 8) sacral diapophyses rounded; 9) maxillary arch toothed, teeth frequently pointed; 10) alary proc-

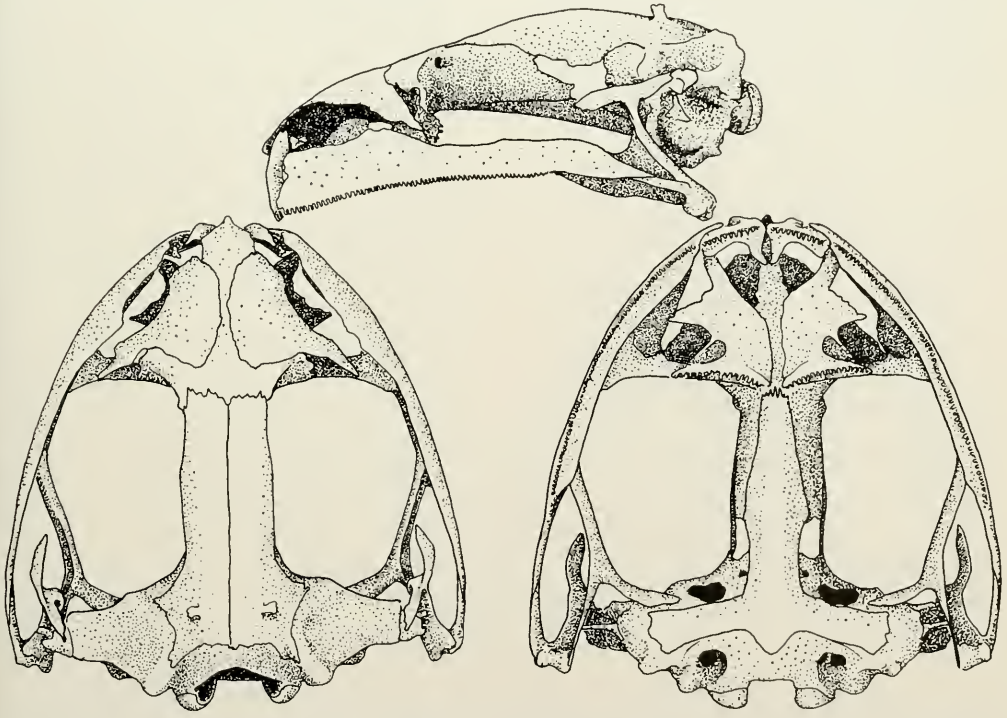

FIGURE 122. Lateral, dorsal, and ventral views of skull of *Leptodactylus quadrivittatus* (KU 41030, × 4), a member of the *fuscus* group.

esses of premaxillae directed dorsally or posterodorsally, broad at base; 11) palatal shelf of premaxilla moderately broad; 12) facial lobe of maxilla relatively shallow, entire maxilla same depth anterior to end of tooth row; 13) palatal shelf of maxilla relatively narrow, no pterygoid process; 14) maxillary arch complete; 15) nasals large, narrowly separated medially; 16) nasals usually not in contact with maxillae, never in contact with pterygoids, nasals have elongate maxillary processes in most species; 17) nasals not in contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals bearing some ornamentation posteriorly in old adults of the larger species; 22) epiotic eminences well defined posteriorly; 23) cristae paroticae moderately long, somewhat stocky; 24) zygomatic ramus of squamosal somewhat expanded, relatively short; 25) otic ramus of squamosal slightly longer than zygomatic ramus, expanded into narrow otic plate which usually rests tenuously on crista parotica; 26) squamosal-maxillary angle less than 45°; 27) columella present; 28) prevomers large, entire, toothed, narrowly separated medially; 29) palatines broad, narrowly separated medially, sometimes bearing odontoid ridge; 30) sphenethmoid extending anteriorly to middle of nasals in *marmoratus, melanonotus, ocellatus,* and *pentadactylus* groups, extending anteriorly to a point anterior to nasals and usually anterior to premaxillae in *fuscus* group; 31) anterior ramus of parasphenoid narrow, not keeled medially, reaching to palatines; 32) parasphenoid alae deflected posteriorly, narrowly overlapped laterally by median rami of pterygoids in *fuscus, melanonotus, ocellatus,* and *pentadactylus* groups, separated in the *marmoratus* group; 33) pterygoids slender, anterior rami reaching to middle of orbit; 34) occipital condyles moderate-sized, not stalked, moderate to wide median separation; 36) terminal phalanges knobbed; 37) alary processes of hyoid on narrow stalks in *fuscus, melanonotus, ocellatus,* and *pentadactylus* groups, wing-like in *marmoratus* group; 39) *m. petrohyoideus anterior* and *m. sternohyoideus* insert on lateral edges of hyoid plate in *fuscus, melanonotus, ocellatus,* and *pentadactylus* groups, insert on hyoid plate near midline in *marmoratus* group; 41) pupil horizontal; 42) males with median subgular or paired lateral vocal sacs or none, males of *fuscus* and *marmoratus* groups lack nuptial asperities, males of *melanonotus, ocellatus,* and *pentadactylus* groups have spines on the thumb, males of the *pentadactylus* group have spines on the chest and thumb; 43) body with diffuse ventral and flank glands or not, many species have glandular folds on the dorsum, species of the *pentadactylus* group have inguinal glands; 44) tongue large, with two long posterior horns; 45) toes not webbed, species of the *melanonotus* and *ocellatus* groups have lateral fringes on the toes, metatarsal tubercles not enlarged, digital tips narrow, first finger slightly longer than second in *marmoratus* group, much longer than second in other species groups except for a few species in the

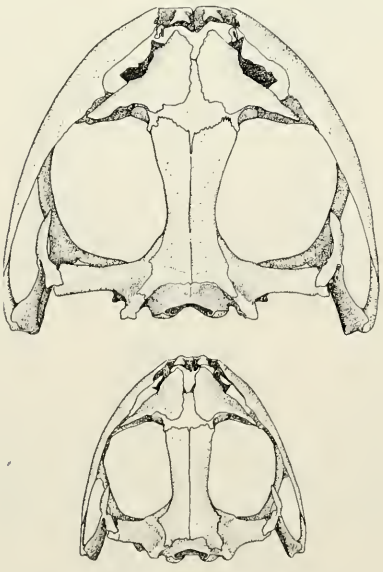

FIGURE 123. Dorsal views of skull of (top) *Leptodactylus pentadactylus* (KU 68159, × 1) and *L. wagneri* (KU 104389, × 1).

melanonotus group; 46) frogs of *marmoratus* group do not have tadpoles, in other groups larvae with median vent, 2/3 tooth rows, labial papillae broadly interrupted anteriorly; 48) eggs laid in foam nest floating on water in *melanonotus, ocellatus,* and *pentadactylus* groups, in these groups the eggs are small and numerous; in the *fuscus* group eggs are deposited in a foam nest in an underground burrow and hatch when the nest is inundated; in the *marmoratus* group the eggs are large, few in number, and are deposited in an underground nest in foam; development is direct in the *marmoratus* group but the other groups have aquatic larvae; 49) adults range in size from 20-200 mm. SVL; 50) tympanum visible externally or concealed.

Composition.—Gorham (1966) listed 60 species in the genus. Of these, three belong to other genera (*L. gaigeae*= *Paratelmatobius gaigeae; L. pulcher*= *Barycholos pulcher; L. tuberculosus*= *Ischnocnema quixensis).* Heyer (1969a) recognized only 32 species. His system is admittedly conservative, but is a considerable improvement over that presented by Gorham.

Distribution.—Middle American lowlands from Sonora, México, and southern Texas to the Argentine Chaco and Guayas region of Ecuador in South America, and on the Lesser Antilles and Hispaniola. All localities for the species of the genus are lowland (usually below 1200 meters).

Remarks.—No new generic synonyms are added here. The generic synonymy of *Leptodactylus* has been stable for many decades, because the genus is rather morphologically uniform in external characteristics. Heyer (1969a) solved many systematic problems of the genus, among which was the discovery of the identity of *Plectromantis wagneri.* This species is a widespread species of the Amazon Basin and has accumulated nearly a dozen synonyms.

I studied the skeletons of 18 species of the genus in formulating my concepts

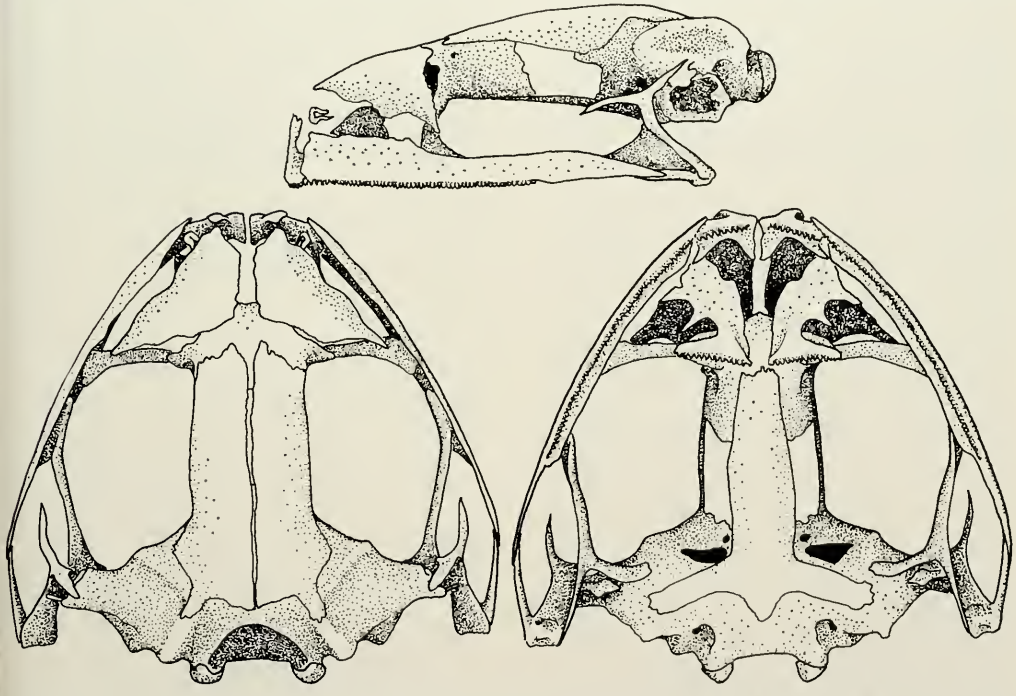

FIGURE 124. Lateral, dorsal, and ventral views of skull of *Leptodactylus hylaedactylus* (KU 119387, × 5).

of the genus. This study illustrated the remarkable osteological homogeneity of the frogs of this genus. Accordingly, I do not advocate the use of subgenera such as those proposed by A. Lutz (1930). Lutz placed the species of the genus in six subgenera; of these, two are generic homonyms, one is a valid generic name of Asiatic ranids *(Platymantis),* and one *(Plectromantis)* was based on erroneous data.

A major advancement in the systematics of this genus was provided by Heyer, who divided the genus into five species groups based on external morphology, thigh musculature, jaw musculature, developmental patterns and tadpole morphology, some osteological characters, and vocalization. Heyer utilized secondary sex characters in his classification; his classification appears to be a realistic one. I contend that his *melanonotus* group is a composite with part of the species (those with arched prevomerine dentigerous processes of the prevomerine bones) being members of the *ocellatus* group.

Heyer advocated placing the *marmoratus* group in a separate subgenus, *Adenomera;* this action is one of preference, but in keeping with the criteria followed throughout this review of the family, I choose not to recognize the subgenus. The frogs of the subgenus *Adenomera* differ from those of the subgenus *Leptodactylus* in that the former exhibit direct development whereas the latter have aquatic tadpoles. Heyer cited additional characteristics to distinguish the *marmoratus* group from other *Leptodactylus* but these additional characters are shared by some other species groups. The musculature of the hyolarynx of the frogs of the *marmoratus* group is like that seen in *Physalaemus* and *Pseudopaludicola* (the criniine pattern). The frogs of the *marmoratus* group resemble *Barycholos pulcher* (see following account) in some but not all morphological characters. When the breeding biology of all of the genera of the Leptodactylinae becomes known, the generic status of *Adenomera* and *Barycholos* should become more apparent.

Barycholos Heyer, 1969
(Fig. 125)

Barycholos Heyer, 1969, Cont. Sci. Los Angeles Co. Mus., 155:6 [Type-species by original designation, *Leptodactylus pulcher* Boulenger, 1898].

Diagnostic definition.—1) sternum containing a calcified style, bifurcate posteriorly; 3) transverse processes of posterior presacral vertebrae slightly shortened; 4) cervical cotylar arrangement type I; 7) omosternum moderate-sized, manubrium elongate, partly calcified; 8) sacral diapophyses slightly dilated; 9) maxillary arch toothed; 10) alary processes of premaxillae directed dorsally, broad at base; 11) palatal shelf of premaxilla relatively deep, deeply incised; 12) facial lobe of maxillae relatively shallow; 13) palatal shelf of maxilla broad anteriorly, narrowing posteriorly, no pterygoid process; 14) maxillary arch complete; 15) nasals large, in broad median contact; 16) nasals narrowly separated from maxillae, widely separated from pterygoids; 17) nasals in tenuous contact with frontoparietals; 18) frontoparietal fontanelle lacking; 19) frontoparietals not ornamented; 22) epiotic eminences moderately well defined; 23) cristae paroticae relatively short, stocky; 24) zygomatic ramus of squamosal relatively short, broadly separated from maxilla; 25) otic ramus of squamosal relatively long, expanded medially to form small otic plate; 26) squamosal-maxillary angle 55°; 27) columella present; 28) prevomers small, irregular in outline, widely separated medially, bearing large, arched, transverse, toothed, dentigerous processes; 29) palatines slender, lacking odontoid ridge; 30) sphenethmoid entire, extending anteriorly beneath nasals; 31) anterior ramus of parasphenoid narrow, not keeled, reaching prevomerine dentigerous processes; 32) parasphenoid alae oriented at right

angles to anterior ramus, not overlapped laterally by median rami of pterygoids; 33) pterygoids small, all rami slender, anterior rami not reaching middle of orbit; 34) occipital condyles small, not stalked, widely separated medially; 36) terminal phalanges T-shaped; 37) alary processes of hyoid plate small, on narrow stalks; 38-39); 41) pupil horizontal; 42) males lacking nuptial asperities, vocal sac large, external, median, subgular; 43) body lacking glands; 44) tongue round, posterior edge free; 45) toes lacking webs and lateral fringes, outer metatarsal tubercle present, inner metatarsal tubercle not enlarged, digital tips dilated, no circumferential groove on discs, first finger much longer than second; 46-48); 49) adults small, about 25 mm. SVL; 50) tympanum visible externally.

Composition.—Monotypic, *B. pulcher.*

Distribution.—Pacific lowlands of Ecuador (Heyer, 1969b).

Remarks.—In external appearance, *Barycholos pulcher* is simply a small *Leptodactylus* of the *marmoratus* group. Heyer (1969b) concluded that *Barycholos* is not closely allied to *Leptodactylus* or *Lithodytes*, but is most closely related to *Eleutherodactylus*. He did not consider the relationship between *Barycholos* and *Eleutherodactylus* to be close.

Barycholos pulcher exhibits the following characteristics which are more *Eleutherodactylus*-like than *Leptodactylus*-like: 11), 15), 22), 32), and 36). *Barycholos* more closely resembles *Leptodactylus* in the following characteristics: 1), 13), and 45). Heyer (1969b) suggested that the life history of *Barachylos* is more like that of *Eleutherodactylus* than *Leptodactylus*. Heyer examined a single adult female of *Barycholos pulcher* which contained 43 ova about 2.8 mm. in diameter and concluded that the species probably exhibits direct development. I agree with Heyer on this point, but do not agree that this character, even in coincidence with T-shaped terminal phalanges, indicates a closer relationship to *Eleutherodactylus* than to *Leptodactylus*. Heyer (1969a) characterized the *marmoratus* group of *Leptodactylus* in having "4-25 eggs per nest; egg diameter 2.1-3.0 mm." In preserved *L. hylaedactylus*, females usually contain about 20 eggs. The species of the *marmoratus* group were assigned to the subgenus *Adenomera* by Heyer (1969a, 1969b); the subgenus was in large part defined on the basis of direct development. As pointed out by Cochran (1955: 309), species of the *marmoratus* group

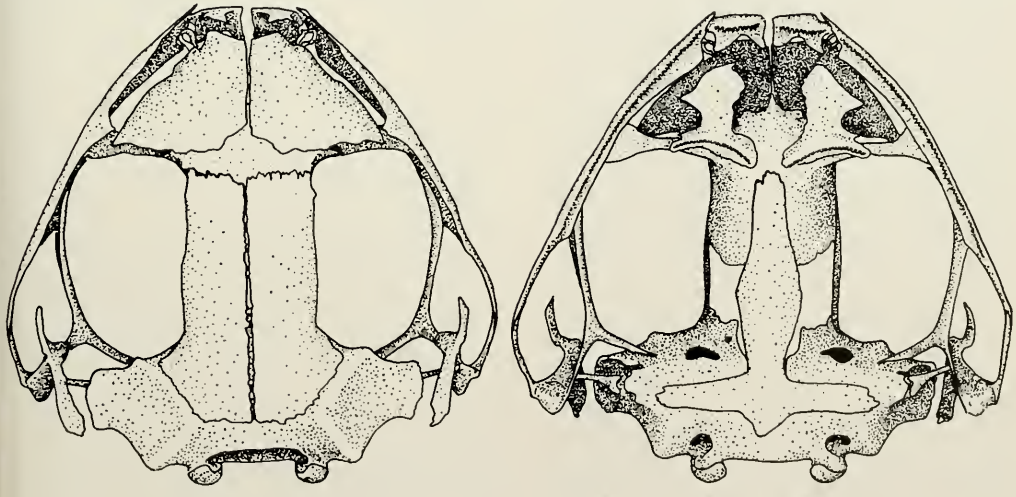

FIGURE 125. Dorsal and ventral views of skull of *Barycholos pulcher* (UMMZ S-2881, × 5.7).

have enlarged digital pads and some indication of T-shaped terminal phalanges. The phalanges are intermediate between the knobbed phalanges of the subgenus *Leptodactylus* and the distinctly T-shaped phalanges of *Eleutherodactylus*, *Heleophryne*, *Lithodytes*, *Sminthillus*, *Syrrhophus*, *Taudactylus*, and *Tomodactylus*. *Barycholos* more closely resembles the subgenus *Adenomera* than *Eleutherodactylus*. Direct development has appeared several times in the course of leptodactylid evolution (for example, *Crinia*, the Eleutherodactylini, the subgenus *Adenomera* of *Leptodactylus*, and the cycloranine genera *Kyarranus* and *Philoria*). The leptodactyline genera *Lithodytes* and *Paratelmatobius* probably exhibit direct development.

The sternal style of *Barycholos* resembles those of the leptodactyline genera (except *Paratelmatobius*) and is very different from the sternal apparatus seen in non-leptodactyline leptodactylid genera. Heyer (1969b) described the style as calcified in contrast to the osseous style seen in *Leptodactylus*. Histologically, the calcified element is a precursor to an osseous one, and the distinction between a calcified and an osseous element cannot be considered of primary importance. The character of the sternal apparatus which can be considered of primary importance is its shape (style-like or plate-like) because this character is not age or size dependent. Because the sternal style of *Barycholos pulcher* is style-shaped, I consider *Barycholos* to be a genus of the Leptodactylinae and to not be closely related to *Eleutherodactylus*.

The relationships of *Barycholos* within the Leptodactylinae are not entirely apparent, but I consider the genus most closely related to the subgenus *Adenomera (Leptodactylus)* and *Lithodytes*. Osteologically, *Barycholos* differs from the former in having larger nasals which are in broad median contact and in having smaller prevomers. *Lithodytes* has large nasals which look like those of *Barycholos* but the prevomers of *Lithodytes* are like those of the *Leptodactylus (Adenomera) marmoratus* group.

PHYLOGENY AND RELATIONSHIPS

Ideally, a discussion of the phylogeny of a group of organisms should be based principally on their fossil record. In the absence of such a chronicle of the evolution of the group, systematists turn to study of the living representatives and infer the phylogeny on the basis of primitive and advanced characters. Many fossils from Cretaceous through Pleistocene horizons have been assigned to the Leptodactylidae. Each of these is discussed below; I consider several of the fossils to represent frogs of families other than the Leptodactylidae. The leptodactylid fossils are too recent to be of any significance in determining phylogeny within the family.

My interpretation of the phylogeny of the Leptodactylidae is principally based on comparisons of the characteristics of pelobatid and leptodactylid frogs. The phylogeny is in large measure deduced from a study of evolutionary trends in many characters. Most of these evolutionary trends were noted by earlier authors; the principle difficulty was determination of the directions of the trends.

THE FOSSIL RECORD

Pleistocene:—Günther (1859b) reported fossils of *Ceratophrys aurita* (as *C. cornuta*), *Leptodactylus ocellatus*, *L. pentadactylus*, and *Leptodactylus* sp. (as *Cystignathus*) from Lagoa Santa, Minas Geraís, Brasil. Rusconi (1932) named *Ceratophrys ensenadensis* from a Pleistocene (Ensenadan) locality near Buenos Aires, Argentina. Mecham (1959) reported late Pleistocene cave deposits in central Texas containing *Hylactophryne augusti* (as *Eleutherodactylus latrans*). Tihen (1960b) and Lynch

(1964) reported middle Pleistocene records for *Syrrhophus marnockii* from northern Texas. Auffenberg (1958) named some specimens from late Pleistocene cave deposits of Barbuda, British Leeward Islands, as *Hyla barbudensis,* which Lynch (1966) placed in the genus *Eleutherodactylus.*

Pliocene:—Ameghino (1899) named *Ceratophrys prisca* from the Upper Pliocene of Monte Hermosa, Argentina.

Miocene:—Casamiquela (1963) named *Wawelia gerholdi* from the Upper Miocene of Río Negro, Argentina, and described additional skeletal remains of *Caudiverbera caudiverbera* (as *Gigantobatrachus parodii*) from the same locality and horizon. The type-specimens of *Gigantobatrachus* were collected from Miocene deposits in Santa Cruz, Argentina (Casamiquela, 1959). Holman (1965) named *Leptodactylus abavus* and reported (1967) *Eleutherodactylus* sp. from the Arikareean, Lower Miocene, of northern Florida.

Oligocene:—Ameghino (1901) listed *Teracophrys* (a *nomen nudum*) from the Upper Oligocene of Patagonia. The specimens are now apparently lost (Schaeffer, 1949). Schaeffer (1949) recorded *Caudiverbera caudiverbera* (as a new species, *Calyptocephallela canqueli*), *Eupsophus* sp., and *Neoprocoela edentata* from Lower Oligocene deposits in Chubut, Argentina.

Eocene:—Schaeffer (1949) named *Caudiverbera casamayorensis* (as a new genus, *Eophractus*) from the Lower Eocene of Chubut, Argentina. Hecht (1960) named *Eorubeta nevadensis* from the Lower Eocene of Nevada. Noble (1930) concluded that *Rana pusilla* Owen, 1847, from the Eocene (Intertrappean) of peninsular India was a myobatrachine leptodactylid and named a new genus for it *(Indobatrachus).*

Cretaceous:—Estes (1964) reported several bones from the Lance Formation (Upper Cretaceous) of Wyoming as possibly representing leptodactylid frogs; he named none of these. Hecht (1960) suggested that some of the frog fossils from the Trinity Sands (Cretaceous) of Texas were primitive leptodactyloids.

The fossil record is summarized in Table 3. Some of these records require special comment, because they are not leptodactylid frogs. The following is a systematic summary (by subfamily) of the fossils I accept as members of the family Leptodactylidae.

Ceratophryinae:—Upper Miocene to Recent of South America. *Wawelia gerholdi* is not distinguishable from either *Ceratophrys* or *Lepidobatrachus* but is clearly a member of the subfamily (see generic account, p. 112. Three species of *Ceratophrys* are known as fossils; two of these are extinct *(C. ensenadensis* and *C. prisca),* the other species still lives in the same area from which the Pleistocene fossils were recovered. *Teracophrys* may be a ceratophryine, but its taxonomic status must await rediscovery of Ameghino's specimens.

Cycloraninae: No fossil record.

Elosiinae: No fossil record.

Heleophryninae: No fossil record.

Leptodactylinae: Pleistocene to Recent of South America. The three species of *Leptodactylus* (*ocellatus, pentadactylus* and sp.) reported by Günther (1859b) are the only fossils known for the subfamily.

Myobatrachinae: Eocene of peninsular India. *Indobatrachus pusillus* is very similar to *Crinia,* and is probably a leptodactylid. However, before the systematic position of *Indobatrachus* can be fully evaluated, an osteological study must be made of the Arthroleptinae (Ranidae). See the generic account of *Indobatrachus* for further details (p. 103).

Telmatobiinae: Fossils of three tribes are known.

Telmatobiini: Lower Eocene to Upper Miocene of Patagonia. *Caudiverbera* is represented in Lower Eocene, Lower Oligocene, and Upper Miocene deposits of south-central Argentina. The Miocene and Oligocene fossils are regarded as

TABLE 3. Geographic and temporal distribution of the fossil frogs currently considered members of the Leptodactylidae.

	NORTH AMERICA	SOUTH AMERICA	OLD WORLD
PLEISTOCENE	*Eleutherodactylus barbudensis*[a]	*Ceratophrys aurita*	
	Hylactophryne augusti	*C. ensenadensis*	
	Syrrhophus marnockii	*Leptodactylus* sp.	
		Leptodactylus ocellatus	
		L. pentadactylus	
PLIOCENE		*Ceratophrys prisca*	
MIOCENE	*Leptodactylus abavus*	*Wawelia gerholdi*	
	Eleutherodactylus sp.	*Caudiverbera caudiverbera*	
OLIGOCENE		*C. caudiverbera*	
		Eupsophus sp.	
		Neoprocoela edentata	
		? *Teracophrys*	
EOCENE	*Eorubeta nevadensis*	*Caudiverbera casamayorensis*	*Indobatrachus pusillus*
PALEOCENE			
CRETACEOUS	[Lance Formation]		
	[Trinity Sands]		

[a] West Indian: Barbuda, Leeward Islands.

identical with the Recent species (Hecht, 1963), but the Lower Eocene fossils are here recognized as specifically distinct. *Neoprocoela edentata,* an ancestral stock for *Batrachophrynus,* is known from the Lower Oligocene of Patagonia. Tihen (1962b) placed it in *Bufo,* but his action is rejected here (see pp.120-122).

Alsodini: Lower Oligocene of Patagonia. Schaeffer's (1949) *Eupsophus* sp. is the only fossil record for this tribe. Many specimens of the fossil are available but all are incomplete. Further study of these fossils should be made to assess their specific status. The fossil species differs from all Recent species of the genus in apparently having the nasal bones in median contact.

Eleutherodactylini: Pleistocene of Texas and Barbuda Island, Leeward Islands. Three species of this tribe are known as fossils. The West Indian *Eleutherodactylus barbudensis* may be extinct or may be identical with *E. martinicensis* (Schwartz, 1967). The Pleistocene records of *Syrrhophus marnockii* occur 200 miles north of the present northern limit of the range of the species (Lynch, 1970a). The fossil of *Hylactophryne augusti* is from a Late Pleistocene cave deposit within the present geographic range of the species.

I do not consider the other species listed in Table 3 to be members of the Leptodactylidae. The fossils here removed from the family have been reported from deposits in North America (Lower Miocene to Upper Cretaceous).

Eleutherodactylus sp.: Holman (1967) referred one right ilium from the Thomas Farm Miocene beds of Gilchrest County, Florida, to the genus *Eleuthero-*

dactylus but because of limited comparative material, did not make a specific assignment. Many, if not most, mainland Central and South American *Eleutherodactylus* have distinct ilial crests in contrast to most West Indian species which have the crest replaced by an ilial ridge. Holman's fossil is similar to the ilia of several West Indian *Eleutherodactylus* but is equally similar to some small specimens of *Acris* which I have examined. Referral of the fossil to the Leptodactylidae cannot be justified; it is equally likely that the fossil represents a young individual of *Acris*, especially in light of Holman's fossil species, *A. barbouri*, from the same locality.

Leptodactylus abavus Holman, 1965: *Leptodactylus abavus* Holman (Lower Miocene of Florida) is a species of *Rana* and may not be separable from *Rana miocenica* Holman of the same horizon and locality. The reasons for placing the species in *Rana* are presented in the account on pelvic girdles (p. 63).

Eorubeta nevadensis Hecht, 1960. The fossils of this frog are preserved as organic imprints in an oil well core. In this condition, the fossils are badly crushed and must be studied under ultraviolet light. Hecht (1960) considered the presence of maxillary teeth and long transverse processes of the posterior presacral vertebrae as characters adequate to associate the fossil with the advanced frogs (Hylidae, Leptodactylidae, and Ranidae). The Bufonidae were not considered because the fossil has a toothed maxilla. The sacral diapophyses of the fossil are dilated and oriented at right angles to the sagittal line; therefore, Hecht reasoned that the fossil did not belong to the Ranidae.

Hecht then looked for hylid and leptodactylid frogs with long transverse processes of the posterior presacral vertebrae and dilated sacral diapophyses. He characterized hylids as having either somewhat shortened or very thin, needlelike transverse processes of the posterior presacral vertebrae. By process of elimination, Hecht assigned the fossil to the Leptodactylidae. Among the leptodactylids available to him, he concluded that the fossil was most similar to *Mixophyes* and *Lechriodus*, because both genera have dilated sacral diapophyses and long transverse processes of the posterior presacral vertebrae. Hecht stated that *Eorubeta* differed from both of these genera in having seven instead of eight presacral vertebrae; *Eorubeta* was further distinguished from *Lechriodus*, because the latter has transverse processes on the atlas. The "atlas" (in the sense of Hecht) of *Lechriodus* is the fused cervical and second vertebrae.

Hecht rightfully complained of a lack of skeletons of representative Recent genera in museums and the lack of comparative osteological studies of Recent frog families. With these restrictions, Hecht's action in assigning the fossil to the Australian section of the Leptodactylidae seems capricious. My study of *Eorubeta* was limited to the description, remarks, and illustrations in Hecht's (1960) paper.

Hecht's description is reasonably accurate. However, I consider the fossil to have eight presacral vertebrae (Hecht recorded seven). Seven presacral vertebrae are clearly evident and all of these bear long transverse processes which are as long as or only slightly shorter than the sacral diapophyses. In all Recent frog genera I have examined, the transverse processes of the second vertebra (first post-cervical) are invariably shorter than those of the third vertebra. The transverse processes of the third vertebra are as long as, or longer than, those of any other presacral vertebra, and are usually somewhat curved. The transverse processes of the right side of the anterior presacral vertebrae of *Eorubeta* are concealed beneath matrix except for the leading edge of the vertebra I consider to be the third (Hecht considered this vertebra to be the second). The remains of the skull overlie parts of the vertebral column in this region. It is

clearly evident from an examination of Hecht's figures, that the transverse processes of vertebra 2 are very long (as long as the sacral diapophyses) and slightly curved. If this vertebra is the second as Hecht contends, then *Eorubeta* has a vertebral column like no other in the Anura. It is more reasonable to suggest that this vertebra is the third. Just anterior to the left transverse process of this vertebra and the scapula, is a small area of bone which Hecht tentatively suggested is the coracoid. This structure might be the left transverse process of the second vertebra. Another interpretation is possible for the bones Hecht called the squamosals, occipital condyles, and foramen magnum. If the "occipital condyles and foramen magnum" are the centrum and neural arch of the second vertebra, then the "squamosals" are of the proper shape and length to be considered the transverse processes of the second vertebra. If this interpretation is correct, then the cervical is not distinguishable from the bones of the posterior part of the skull. The structure designated "atlas" by Hecht is much too small to be this element and is probably not a complete bone. Pending the recovery of additional specimens, I will not offer further interpretation of the osteology of *Eorubeta nevadensis.*

I concur with Hecht that the fossil does not represent the Ascaphidae, Discoglossidae, Pipidae, or Rhinophrynidae, for his reason (the transverse processes of the posterior presacral vertebrae in the Recent genera of these families are very short and often knob-like). The fossil has dilated sacral diapophyses which are unlike those of any ranid known to me. The Dendrobatidae and leptodactylids of the subfamily Elosiinae have non-dilated sacral diapophyses and short transverse processes on all presacral vertebrae. The pelobatids of the subfamilies Pelobatinae and Pelodytinae have very short transverse processes on the posterior presacral vertebrae, as do some Australo-Papuan leptodactylids, and thus could not be closely related to the fossil frog. The other frog families have dilated sacral diapophyses in some or all of the included genera (Bufonidae, Centrolenidae, Hylidae, Leptodactylidae, Megophryinae, Microhylidae and Pseudidae). The only skeletal elements of *Eorubeta nevadensis* which are useful in comparisons are those of the vertebral column, ilium, and maxilla. *Eorubeta* does not closely resemble any genus in the seven families listed above. *Eorubeta* has maxillary teeth and therefore is probably not a bufonid, although this character need not completely eliminate the Bufonidae from consideration. The ilium of *Eorubeta* has little indication of a dorsal protuberance, prominence, or ilial crest; this condition is seen in some leptodactylids, megophryine pelobatids, and microhylids. The ilium is not exposed in lateral aspect and therefore centrolenids and hylids cannot be eliminated from consideration. *Eorubeta* is not a bufonid, ceratophryine, telmatobiine, leptodactyline, or pseudid because the ilia of *Eorubeta* lack large ilial prominences and/or dorsal crests.

The vertebral skeletons of the remaining groups (Centrolenidae, Hylidae, Cycloraninae, Heleophryninae, Myobatrachinae, Microhylidae, and Megophryinae) are difficult to separate as units when the details of the cervical vertebra are unknown. The cervical cotyles are widely separated medially in the Centrolenidae, Hylidae, Microhylidae, and Myobatrachinae, whereas the cotyles are narrowly separated in the Cycloraninae, Heleophryninae, and Megophryinae. The cervical vertebra is not distinguishable in *Eorubeta.* The only genera of the seven family groups listed above with the transverse processes of the posterior presacral vertebrae as long as the sacral diapophyses are *Hemiphractus* and some *Hyla* (Hylidae), *Batrachophrynus, Lechriodus, Limnodynastes,* and *Mixophyes* (Leptodactylidae, Telmatobiinae and Cycloraninae), and *Megophrys* (Pelobatidae, Megophryi-

nae). The transverse processes of *Batrachophrynus* (Fig. 79) are very similar in bulk to those of *Eorubeta,* but the sacral diapophyses of these two genera are very different from one another. *Eorubeta* is unique, insofar as I am aware, in having wide, dilated sacral diapophyses. The only comparable sacral diapophyses known to me are those of *Atelopus* and *Rhinoderma.*

In summary, *Eorubeta* does not closely resemble the skeleton of any known modern frog genus and cannot be assigned to any presently recognized family on the basis of its known morphology. Hecht's (1960) assignment of *Eorubeta* to the Leptodactylidae is not defensible and probably in error. The only reasonable systematic assignment of the fossil is to "Family *incertae sedis,* Order Salientia."

Estes (1964) described and figured several Upper Cretaceous frog fossils from the Lance Formation of Wyoming.[13] Among the fossils which are of significance to this discussion are the following: "Family ?Pelobatidae; Suborder Neobatrachia, Family *incertae sedis,* near Hylidae?; and Family *incertae sedis,* near Leptodactylidae?" (Estes, 1964: 57-61, figs. 30-32). The coccyx described and figured by Estes is unquestionably that of a megophryine pelobatid, although a generic assignment is not possible at present. The ilium described and figured by Estes is not sharply distinguishable from the ilia of some species of *Pelobates* and *Scaphiopus,* but is different from the ilia of most Megophryinae and Pelodytinae. The incomplete left maxilla described and figured by Estes resembles those of *Pelobates, Scaphiopus,* and, insofar as it is known, that of *Eopelobates.*

Estes tentatively assigned an incomplete right squamosal to the Leptodactylidae. The squamosal does not resemble that of any extant leptodactylid genus but is similar to the squamosals of *Scaphiopus (Scaphiopus)* and some *Pelobates.* Estes remarked that the fossil has an "opisthotic articulation surface [which] resembles that of leptodactylids." This cryptic statement implies that there is (or are) a characteristic opisthotic articulation of the squamosal in leptodactylids; the statement is not in agreement with my observations. A complete spectrum of opisthotic articulations can be demonstrated within the Leptodactylidae, ranging from species lacking the dorsal portion of the squamosal *(Notaden)* to those with the squamosal enclosing much of the crista parotica *(Caudiverbera, Ceratophrys).* Estes (1969) subsequently assigned this squamosal as well as numerous other Late Cretaceous and Paleocene bones to *Scotiophryne pustulosa* (Discoglossidae). Further comment on this action is deferred to a separate paper. The two bones (squamosal, figured; and nasal) which Estes (1964) suggested might be from hylids or leptodactylids, could equally confidently be assigned to the Pelobatidae.

The pelobatid centrum from the Middle Eocene of Wyoming figured by Hecht (*in* McGrew, 1959) is clearly that of a megophryine pelobatid, and as Hecht pointed out, is very similar to that of *Eopelobates grandis* from the Lower Oligocene of South Dakota. Hecht's fossil is probably generically identical with *Eopelobates grandis* and may not be specifically distinct. Estes' megophryine coccyx is possibly representative of the same complex.

Hecht (1960:13) referred to some fossil frogs from the Trinity Sands of Texas (early Cretaceous) as "a primitive leptodactylid or some close relative." Until he publishes on them, no further comment will be made, although it should be born in mind that Hecht considered *Eorubeta* a definite leptodactylid. Hecht and Estes (1960) named a Jurassic frog as *Comobatrachus* and placed it in Reig's (1958) Neobatrachia.

[13] Estes (1970) associated a number of these Late Cretaceous elements with the genus *Eopelobates* (Pelobatidae, Megophryinae).

They further suggested that the fossil not be assigned to any recognized family but that "on the basis of probability [no confidence limits are given] a leptodactyloid affinity appears more likely [than a microhylid or hyperoliid affinity]."

The fossil record for the Leptodactylidae can be summarized as follows: fossils of several stocks are known from the Tertiary of southern South America; an Eocene frog from peninsular India seems to be a myobatrachine leptodactylid; and leptodactylids are not known elsewhere in the world until the Pleistocene of the West Indies and Texas.

With the exception of *Neoprocoela* and *Indobatrachus,* the fossil record of the Leptodactylidae is of little use in determining the phylogeny and is of limited value in discussing zoogeography.

PELOBATID-LEPTODACTYLID RELATIONSHIPS

Some Papuan leptodactylid frogs have been confused with pelobatid frogs. *Lechriodus* was erroneously believed to be a pelobatid until Noble (1924) demonstrated that the pectoral and thigh musculature were bufonoid, not pelobatoid. In general, however, the two families have always been regarded as being very different from one another. This distinction hinged largely upon a distinction between the Pelobatinae *(Pelobates* and *Scaphiopus)* and the Neotropical leptodactylids. In the former, the coccyx is fused to the sacral vertebra, whereas in leptodactylids the two bones are separate.

The Pelobatidae may be separated from the Leptodactylidae by the greater dilation of the sacral diapophyses in the former, the sacral-coccygeal articulation (fused or with a single condyle in former, double condyle in latter), middorsal cricoid gap in former, single slip to *m. depressor mandibulae (pars scapularis)* in former, and *m. semitendinosus* and *m. sartorius* not separate in former. Two or three subfamilies are recognized depending on the author: Pelobatinae, Megophryinae, and sometimes Pelodytinae.

The Pelobatidae are unquestionably the more primitive group (Griffiths, 1963; Inger, 1967; Kluge and Farris, 1969; Noble, 1922, 1931; and Tihen, 1965), but the distinction between the two families is not so great as has been previously believed, principally because previous authors have tended to ignore the similarities between the Megophryinae and the Australo-Papuan leptodactylids and to stress those features which distinguish the two most abundant and best known groups of the two families (the Pelobatinae and Neotropical leptodactylids).

The amplectic position of the male in the Pelobatidae, Cycloraninae and Myobatrachinae is inguinal in contrast to the axillary amplexus in almost all advanced frogs. The Megophryinae, Myobatrachinae and Cycloraninae (part) have free intervertebral discs, a character that has been regarded as paedomorphic or specialized by most authors but which is more likely primitive (Tihen, 1965). Several other characteristics, some heretofore regarded as of little significance, occur in the primitive families and in some leptodactylids and sporadically, though rarely, in advanced frogs [e.g., absence of an outer metatarsal tubercle; vertical pupil; large, juxtaposed occipital condyles; small transverse processes on the posterior presacral vertebrae; imbricate neural arches; and tadpoles with complete row(s) of labial papillae and high number of anterior tooth rows (3-6)].

Griffiths (1963) contended that ectochordal and stegochordal centra were primitive to holochordal centra; Inger (1967) argued that holochordy is probably primitive since it occurs in most extinct lepospondylous amphibians and that therefore ectochordy and stegochordy are derived. Ectochordy has been termed paedomorphic; if so, then any distinction between frog families based on the nature of the coccygeal-

sacral articulation cannot be seriously considered in interpreting the macrosystematic evolution of frogs. A full range of variation occurs in the Pelobatidae—the ectochordal megophryines exhibit a monocondylar articulation, the stegochordal pelobatines exhibit a coccygeal-sacral fusion, and the presumably stegochordal pelodytines exhibit a bicondylar articulation. Imbricate neural arches occur in all pelobatids and are found in cycloranines (but not myobatrachines), in heleophrynines, in ceratophryines, and in some telmatobiines (Odontophrynini and Telmatobiini). The degree of dilation of the sacral diapophyses in pelobatids exceeds that seen in any leptodactylid except *Neoprocoela* (Lower Oligocene, Patagonia). Bufonids, which are generally conceded to be leptodactylid derivatives, have broadly dilated sacral diapophyses as well. If *Neoprocoela* is properly assigned familially, then all primitive leptodactylids may have had sacral dilations of the pelobatid degree—those living leptodactylids with sacral dilations do not approach the condition seen in bufonids or pelobatids. The sacral vertebra of *Pelodytes* is more like that of pipids than other pelobatids.

Hecht (1960) mentioned the lack of moderate to long transverse processes on the presacral vertebrae in primitive frogs. My examination of skeletons of all ascaphid, discoglossid, pipid, and rhinophrynid genera confirms his observation. Among the nine living and three extinct pelobatid genera some variation occurs. The transverse processes of the posterior presacral vertebrae are little more than bosses or are very short in *Macropelobates*, *Pelobates* and *Scaphiopus*. *Miopelodytes* and *Pelodytes* have short processes strongly sloped anteriorly as in pipids. In the *Megophrys* and *Eopelobates* (Megophryinae), the transverse processes of the posterior presacral vertebrae are of moderate length (Zweifel, 1956a; personal observation) but they are shortened and directed strongly anteriorly in at least one species of *Leptobrachium* (Boulenger, 1908), recalling the condition seen in *Pelodytes*. The anterior presacral vertebrae of all pelobatids have elongate transverse processes (relative to the widths of the sacral diapophyses) as well as in some primitive leptodactylids (Ceratophryinae). This same condition appears in some bufonids and is variable within *Bufo*. Several groups of leptodactylids have relatively short transverse processes on the posterior presacral vertebrae. This is most pronounced in *Neobatrachus* and *Notaden* (Fig. 30) but is also found in several Neotropical groups (e.g., Telmatobiini, Odontophrynini, and Grypiscini) as well as in *Heleophryne* and most Myobatrachinae and Cycloraninae.

The presence of postzygapophyses on the sacrum and prezygapophyses on the coccyx must be considered primitive. The zygapophyses are not present in *Pelodytes*, and their presence is obliterated by sacral-coccygeal fusion in the Pelobatinae; they are found in the Megophryinae but not consistently in any leptodactylid. McDowell *(in litt.)* observed sacral postzygapophyses and coccygeal prezygapophyses in *Metacrinia* and in the enigmatic *Sooglossus*, but I have seen them only in *Batrachophrynus* and *Megophrys*. Zweifel (1956a) described coccygeal zygapophyses in *Eopelobates*.

The tadpoles of pelobatids and leptodactylids, as well as of all advanced frogs (except the microhylids whose relationships are obscure), are Type IV of Orton (1953). Admittedly, use of gross tadpole morphology as a basis of macrosystematic (interfamilial) classification is hazardous (e.g., Inger, 1967), but an examination of intrafamilial variation can be useful in determining intrafamilial evolutionary trends. Inger (1967) characterized the Pelobatidae and Leptodactylidae as having tadpoles with median vents. Orton (1952) characterized the pelobatid tadpoles as follows: vent median, beak present, tooth rows usually

divided with one complete short row anteriorly and two complete rows posteriorly, and labial papillae complete except for a narrow median interruption anteriorly. The data for pelobatids, insofar as is known, are summarized in Table 4.

Only half of the pelobatid genera (and species) have median vents; the temperate Himalayan genera have dextral vents as does the subtropical and tropical *Leptobrachium*. Inger's (1966: 25) statement that a complete row of papillae across the upper lip is characteristic of pelobatids is in error. Insofar as I am aware, it is true for only *L. gracilis* and *L. pelodytoides,* although some *Oreolalax* have large, widely scattered papillae across the upper lip (Liu, 1950). The uppermost tooth row is complete in all pelobatids (if teeth are present) and is very short in the Pelobatinae and Megophryinae. In *Pelodytes* this row is almost as wide as the mouth, recalling the condition seen in most tadpoles. The Pelobatinae and Pelodytinae differ from the Megophryinae in having two complete tooth rows across the fully papillate lower lip; only a single complete row is found in megophryines. Most tooth rows are divided medially by the upper beak in pelobatids. This feature in combination with the usually high tooth formula characterizes most pelobatids. This is not to say that this condition is not duplicated elsewhere; for example, *Neobatrachus* has a dental formula of I:2-2/1-1:II to I:3-3/1-1:II, *Mixophyes* has a II:4-4/1-1:II with three other very short lateral divided rows posteriorly and *Heleophryne* has a IV/1-1: XII to IV/1-1:XVI formula; most bufonoids exhibit a I:1-1/III tooth formula.

The tadpoles of pelobatids suggest a closer relationship between the European and North American genera than either group has to the Megophryinae. However, the variation within the Megophryinae suggests that the tadpole can be a hazardous source for definitive statements about relationships. Among bufonoid frogs the high tooth formulae in cycloranine and heleophrynine leptodactylids is suggestive of the pelobatid condition in distinction to the relatively dissimilar mouthparts seen in other bufonoid frogs. Tadpole morphology represents perhaps one of the most useful and most misused of the available character complexes to be used in frog classification. A major problem to be overcome is the descriptive formulae applied to the mouth parts. Many authors use the most simple, least informative system

TABLE 4. Characteristics of Recent pelobatid genera—tadpoles[a]

Genus	Vent median	Labial papillae complete anteriorly	Tooth formula (Low - High)
Scaphiopus[b]	X	O	II:1-1/2-2:II—I:4-4/4-4:II
Pelobates	X	O	I:3-3/3-3:II
Pelodytes	X	O	I:3-3/3-3:II
Nesobia	?	?	?
Megophrys	X	A[c]	0
Leptobrachium	O	V	0 —1:7-7/5-5:I
Oreolalax	O	O	I:4-4/4-4:I—I:7-7/7-7:I
Scutiger	O	O	I:3-3/4-4:I—I:6-6/6-6:I
Vibrissaphora	O	O	I:5-5/4-4:I

[a] *Data* from Boulenger (1897), Inger (1966), Liu (1950), Orton (1952), Pope (1931), and Stebbins (1951).
[b] Including *Spea.*
[c] Absent.

of arabic numerals separated by a solidus (i.e., 2/3) for tadpoles with all of the rows complete or some of them divided. Using various systems, the dental formula for *Vibrissaphora liui* could be presented as:

(A) 6/5
1

(B) $\frac{5\text{-}5}{4\text{-}4}$
1

(C) I:5-5/4-4:I

(D) 1C, 1D, 4L/1L, 3D, 1C

The formula with the greatest information content is the last (D), in which the arabic numeral preceding the letters C, D, and L refers to the number of complete, divided (but not lateral), and lateral (and divided) rows of teeth respectively. Lateral rows are separated by the beak. This system differs from that of Liu (1950) in distinguishing between divided and lateral rows and does not require the use of Roman numerals. Liu's system is preferable to the 4-layered formula (B) in requiring less space on a printed page. The four-layered formula likewise does not distinguish divided from strictly lateral rows although this distinction can be demonstrated to be two ends of a continuum.

There can be little argument against the statement that the Pelobatidae is the most primitive of the frog families, except the archaic Ascaphidae, Discoglossidae, Pipidae, and Rhinophrynidae (Tihen, 1965). An appropriate test of which of the advanced families is most closely related to the Pelobatidae would be to compare them relative to the number of primitive characters shared. The selection of characters and determination of evolutionary direction was made on the following bases: 1) characters shared between the Pelobatidae and some or all of the archaic frog families were regarded as unquestionably ancestral; and 2) those characteristics which occur in these archaic families but also occur in some of the bufonoid families were selected as being useful in measuring the relative primitiveness of each of the bufonoid families and subfamilies (and tribes of the leptodactylid subfamily Telmatobiinae).

The family or subfamily with the lowest sum of values is judged to be most primitive, and the higher the sum of values, the greater is the divergence of that group from the ancestral stock. These primitive characters are (I) large, closely approximated occipital condyles —Types II or III; (II) imbricate neural arches; (III) anterior presacral vertebral transverse processes elongate and posterior presacral vertebral transverse processes shortened; (IV) diapophyses of sacral vertebrae broadly dilated; (V) post-zygapophyses on sacral vertebra and prezygapophyses and/or transverse processes present on anterior end of coccyx; (VI) intervertebral discs free; (VII) ilium lacking dorsal crest, ilial prominence or protuberance; (VIII) all skull bones present; maxillaries, premaxillaries, and prevomers toothed; (IX) phalangeal formulae 2-2-3-3 and 2-2-3-4-3; (X) pupil vertical; (XI) outer metatarsal tubercle absent; (XII) amplexus inguinal; (XIII) eggs small, laid in water, tadpole free-living; (XIV) tadpole vent median; (XV) tadpole dental formula including at least three or four rows above and three rows below beak; and (XVI) pectoral girdle arciferal. Each of these 16 characters or character complexes was assigned a value from 0 to 2 for each of the 23 bufonoid and pelobatid taxa. The character states and values are summarized in Table 5 and the scores and sums for 35 family groups of "non-archaic" frogs in Table 6. A value of 0 indicates that the primitive condition is uniform within the group; a value of 1 indicates the group exhibits an intermediate condition or is variable with more than one-half of the included taxa exhibiting the primitive state; and a value of 2 indicates that a majority of or all of the included taxa share the (or a)

derived state for the character. The sum of the values for the 16 characters is an index of how far removed a given taxon is from the basal stock of the Bufonoidea —the Pelobatoidea. All three pelobatid subfamilies exhibit low values—the Megophryinae with 2, the Pelobatinae with 3, and the Pelodytinae with 4. The following leptodactylid groups exhibit values below 14—Heleophryninae, Cycloraninae, Ceratophryinae, and Telmatobiini (Telmatobiinae). The Heleophryninae are only slightly removed from the pelobatid zone and are considerably more primitive than any other group of the "higher frogs." The Cycloraninae are well removed from the pelobatid zone but less than one-half as far removed as are the Myobatrachinae. The leptodactylids of southern South America (Ceratophryinae and telmatobiine and alsodine Telmatobiinae) are more primitive than any other bufonoid groups (except the heleophrynine and cycloranine leptodactylids). Of the nonleptodactylid bufonoid families and subfamilies, the Phyllomedusinae are least unlike the pelobatoid ancestor. The Bufonidae, which are usually regarded as only slightly advanced over the Leptodactylidae, are the next most primitive group.

TABLE 5. Sixteen phylogenetically significant characters, their character states and values.

I.	Cervical type II = 0
	Cervical type I = 2
II.	Neural arches imbricate = 0
	Neural arches open = 2
III.	Transverse processes of anterior presacral vertebrae expanded, those of posterior presacral vertebrae shortened = 0
	All transverse processes as long as sacral diapophyses or all transverse processes shorter than sacral diapophyses = 2
IV.	Sacral diapophyses dilated = 0
	Sacral diapophyses rounded = 2
V.	Sacral vertebra bearing postzygapopyses and/or coccyx bearing prezygapophyses = 0
	Sacral vertebra lacking postzygapophyses and coccyx lacking prezygapophyses = 2
VI.	Intervertebral discs free = 0
	Intervertebral disc fused to centrum = 2
VII.	Ilium without dorsal crest or dorsal protuberance = 0
	Ilium with dorsal crest and/or dorsal protuberance = 2
VIII.	All skull bones present, premaxillae and maxillae bearing teeth = 0
IX.	Phalangeal formulae normal = 0
	Some skull bones lost and/or premaxillae and maxillae toothless = 2
	Intercalary element present or phalanges lost = 2
X.	Pupil vertical = 0
	Pupil horizontal or round = 2
XI.	No outer metatarsal tubercle = 0
	Outer metatarsal tubercle present = 2
XII.	Amplectic position inquinal = 0
	Amplectic position axillary = 2
XIII.	Eggs small, usually pigmented, larvae aquatic = 0
	Eggs large, development abbreviated or direct = 2
XIV.	Tadpole vent median = 0
	Tadpole vent dextral = 2
XV.	Larval tooth formula at least 3/3 = 0
	Larval tooth formula less than 3/3 = 2
XVI.	Pectoral girdle arciferal = 0
	Pectoral girdle firmisternal = 2

The Pelobatidae are intermediate between the primitive (discoglossoid and pipoid) and the advanced (bufonoid and ranoid) frogs. The leptodactylids are the stem bufonoids and are difficult to separate from the pelobatids.

TABLE 6. Values for each of the sixteen phylogenetically significant characters in non-archaic frog groups.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	Sum
Pelobatidae																	
Megophryinae	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2
Pelobatinae	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	3
Pelodytinae	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	0	4
Leptodactylidae																	
Heleophryninae	0	0	1	2	2	1	0	0	0	0	0	?	0	0	0	0	6
Cycloraninae	0	0	1	1	2	1	1	0	0	1	0	0	0	1	1	0	9
Myobatrachinae	2	2	1	1	1	0	1	1	0	2	2	0	0	2	2	0	17
Ceratophryinae	0	0	0	2	2	2	1	0	0	1	1	2	0	0	1	0	12
Telmatobiini	0	0	1	1	2	2	1	0	0	1	1	2	0	0	2	0	13
Alsodini	1	1	1	1	2	2	1	0	0	2	2	1	0	0	2	0	16
Odontophrynini	1	0	2	2	2	2	1	0	0	2	2	2	0	0	2	0	18
Leptodactylinae	2	1	2	2	2	2	2	0	0	2	2	2	0	1	2	0	22
Elosiinae	2	2	2	2	2	2	2	1	0	2	2	2	0	2	2	0	25
Grypiscini	2	2	2	2	2	2	2	0	0	2	2	2	1	2	2	0	25
Eleutherodactylini	2	2	2	2	2	2	2	0	0	2	2	2	2	2	2	0	26
Bufonidae	0	1	2	1	2	2	2	2	0	2	2	2	0	1	2	1	22
Rhinodermatidae	0	2	2	1	2	2	2	2	0	2	2	2	2	0	2	2	25
Centrolenidae	2	2	2	1	2	2	2	1	2	2	2	2	1	0	2	0	25
Hylidae																	
Phyllomedusinae	2	0	2	0	2	2	2	0	1	0	2	2	1	1	2	0	19
other Hylidae	2	2	2	2	2	2	2	1	1	2	2	2	2	2	2	0	28
Dendrobatidae	2	2	2	2	2	2	2	2	0	2	2	2	1	1	2	2	28
Pseudidae	2	2	2	2	2	2	2	0	2	2	2	2	2	2	2	0	28
Sooglossidae	2	2	2	2	0	0	?	?	0	2	0	?	2	0	2	2	16+
Ranidae																	
Raninae	2	2	2	2	2	2	2	0	0	2	2	2	0	2	0	2	24
Rhacophorinae	2	2	2	2	2	2	2	0	2	2	1	2	1	2	0	2	26
Petropedetinae	2	2	2	2	2	2	2	0	0	2	0	2	0	2	0	2	22
Hemisinae	?	?	?	2	2	2	?	2	2	0	0	2	0	2	0	2	16+
Hyperoliidae																	
Astylosterninae	2	2	2	2	2	2	2	0	2	1	0	2	0	2	0	2	23
Hyperoliinae	2	2	2	2	2	2	2	0	2	0	0	2	0	2	0	2	22
Arthroleptinae	2	2	2	2	2	2	2	0	2	2	2	2	2	0	2	2	28
Microhylidae																	
Dyscophinae	?	0	?	0	2	2	0	0	0	1	0	2	0	0	2	2	11+
Brevicipinae	?	0	?	0	2	2	?	2	0	2	2	0	2	0	2	2	16+
Asterophryinae	2	0	2	0	2	2	0	2	0	2	0	2	2	0	2	2	20
Microhylinae	2	0	0	0	2	2	1	1	0	2	0	2	0	0	2	2	16
Cophylinae	2	2	2	0	2	2	0	0	0	2	0	2	2	0	2	2	20
Phrynomerinae	2	2	2	0	2	2	1	2	2	2	0	2	0	0	2	2	23

INTRAFAMILIAL RELATIONSHIPS OF THE LEPTODACTYLIDAE[14]

Figure 126 reveals that the Leptodactylidae exhibit the greatest range of intrafamilial variability or diversity among the Pelobatoidea, Bufonoidea, and Ranoidea. In part, this diversity represents a finer degree of knowledge about the Leptodactylidae than about some other families, but the diversity is also real. The Leptodactylidae have been the convenient "catch-all" for genera of bufonoid frogs with obscure relationships, and can be defined as "those bufonoid frogs that are not members of the Bufonidae, Centrolenidae, Dendrobatidae, Hylidae, Pseudidae, or Rhinodermatidae." The intrafamilial relationships of the Leptodactylidae are schematically summarized in Fig. 127.

The Leptodactylidae can be viewed as a series of increasingly more specialized subfamilies and tribes which bridge the morphological and behavioral gaps between the Pelobatidae and the smaller families of the Bufonoidea and the Ranoidea. The least specialized subfamilies and tribes of leptodactylids occur in southern Africa and the Australo-Papuan region. Other, only slightly more specialized, groups occur in temperate South America, and the very specialized groups occur in the subtropical and tropical zones of South America and Middle America.

The subfamily Heleophryninae contains one genus and is restricted in distribution to southern Africa. *Heleophryne* is the most primitive leptodactylid genus in terms of its degree of divergence from the pelobatids. In some characters, *Heleophryne* resembles some of the genera of Australo-Papuan leptodactylids (*Heleioporus*, *Neobatrachus*, *Notaden*, and *Mixophyes*) of the subfamily Cycloraninae, but the Australo-Papuan genera are closely interrelated, and none shows any evidence of a close relationship with *Heleophryne*. The characteristics shared by *Heleophryne*, some of the Cycloraninae, the Ceratophryinae, and the Telmatobiini reflect those of the ancestral stock(s) of the Leptodactylidae and may be used to demonstrate a close relationship among these eleven genera; however, with the exception of *Heleophryne* and the ceratophryines, the other genera are the primitive members of larger groups. *Heleophryne* may represent an independent line of pelobatid derivatives which has achieved the leptodactylid or bufonoid grade.

The Myobatrachinae are a relatively compact group of Australo-Papuan genera with one Eocene fossil genus from peninsular India. Although sympatric with the Cycloraninae, the Myobatrachinae are not closely related to the Cycloraninae. Other than the characteristics of leptodactylid frogs, the two subfamilies have one unifying character (inguinal amplexus), but this is shared with ascaphids, discoglossids, pipids, rhinophrynids, pelobatids, and *Batrachyla* (Telmatobiinae, Leptodactylidae). I consider it likely that two other genera of leptodactylids will be found to exhibit inguinal amplexus—*Heleophryne* and

[14] Elsewhere (Lynch, MS) I have proposed uniting the Old World leptodactylid subfamilies as the family Myobatrachidae and using Leptodactylidae for the four Neotropical subfamilies. As I noted in the paper to be published in "Evolutionary Biology of the Anura," the Neotropical subfamilies form a well-defined group which is approached by only one Old World subfamily, the Cycloraninae. The Myobatrachinae form a rather isolated group from all other leptodactyloids and could be placed in a family of their own (the Sooglossidae is probably not separable from Myobatrachinae). The cycloranine-heleophrynine relationship is somewhat tenuous and apparently not very close, but these two groups seem to be somewhat more closely related to each other than either is to the myobatrachines or the Neotropical complex.

Using the Leptodactylidae as a single family for all seven subfamilies is only a slightly greater abstraction than to place the Old World subfamilies in one family (Myobatrachidae) and the Neotropical subfamilies in a second (Leptodactylidae). Cladistically more sound would be to use three familes, one for the Myobatrachinae, a second for the Cycloraninae and Heleophryninae, and a third for the Neotropical families. If the latter fragmentation is employed, use of the term leptodactyloid becomes appropriate.

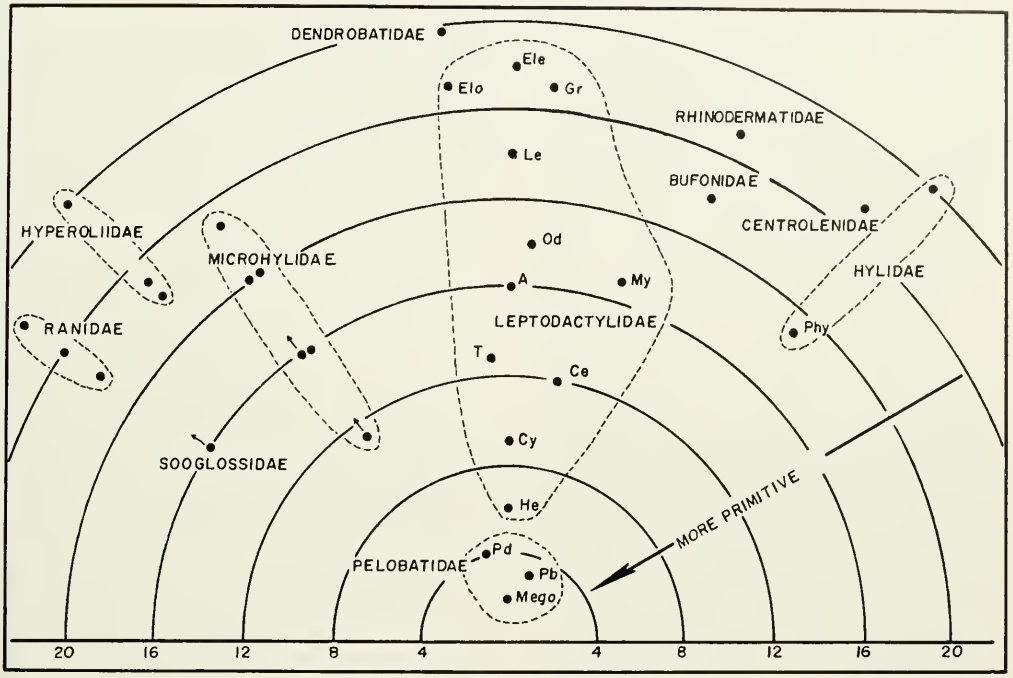

FIGURE 126. Comparison of the relative primitiveness of 35 groups of non-archaic frogs including the 23 bufonoid and pelobatid subfamilies and tribes. The concentric semicircles are guidelines and are not intended to have a special significance. Families are enclosed in dashed lines. The abbreviations used are as follows: A = Alsodini, Ce = Ceratophryinae, Cy = Cycloraninae, Ele = Eleutherodactylini, Elo = Elosiinae, Gr = Grypiscini, He = Heleophryninae, Le = Leptodactylinae, Mego = Megophryinae, My = Myobatrachinae, Pb = Pelobatinae, Pd = Pelodytinae, Phy = Phyllomedusinae, and T = Telmatobiini. The separation of taxa by degrees of arc is not intended to reflect relationships.

Thoropa. The tadpole mouthparts of the Myobatrachinae are unlike those of all other leptodactylids but are very similar to those of the bufonids. It must be stressed that the Myobatrachinae and Bufonidae share few other characters and that the similarity in tadpole mouthparts may well be convergent or parallel. The species of most myobatrachine genera are toothless, but the species of some genera have teeth on the maxillary arch. The myobatrachines have type I cervical cotylar arrangement and widely separated occipital condyles in contrast to the type II cervical cotylar arrangement and narrowly separated occipital condyles of bufonids. Further study must be made to evaluate the closeness of the relationship between these two groups, although among the extant leptodactylids, I consider the myobatrachines as least likely ancestors of the nearly cosmopolitan Bufonidae.

The Cycloraninae are restricted to the Australo-Papuan region, as are the Myobatrachinae. Parker (1940) suggested that with further study, the two subfamilies would be shown to be less distinctive than he had characterized them. However, the additional osteological and tadpole characters utilized here have amplified the distinction between these two subfamilies. As pointed out above, the two Australo-Papuan subfamilies share only one significant character. I consider the community of ancestry of these two groups to be very ancient if it existed at all. The Cycloraninae share some characters with the Telmatobiini, Alsodini, and Ceratophryinae, but are not closely related to any of these groups. The tribe Cycloranini is less unlike the

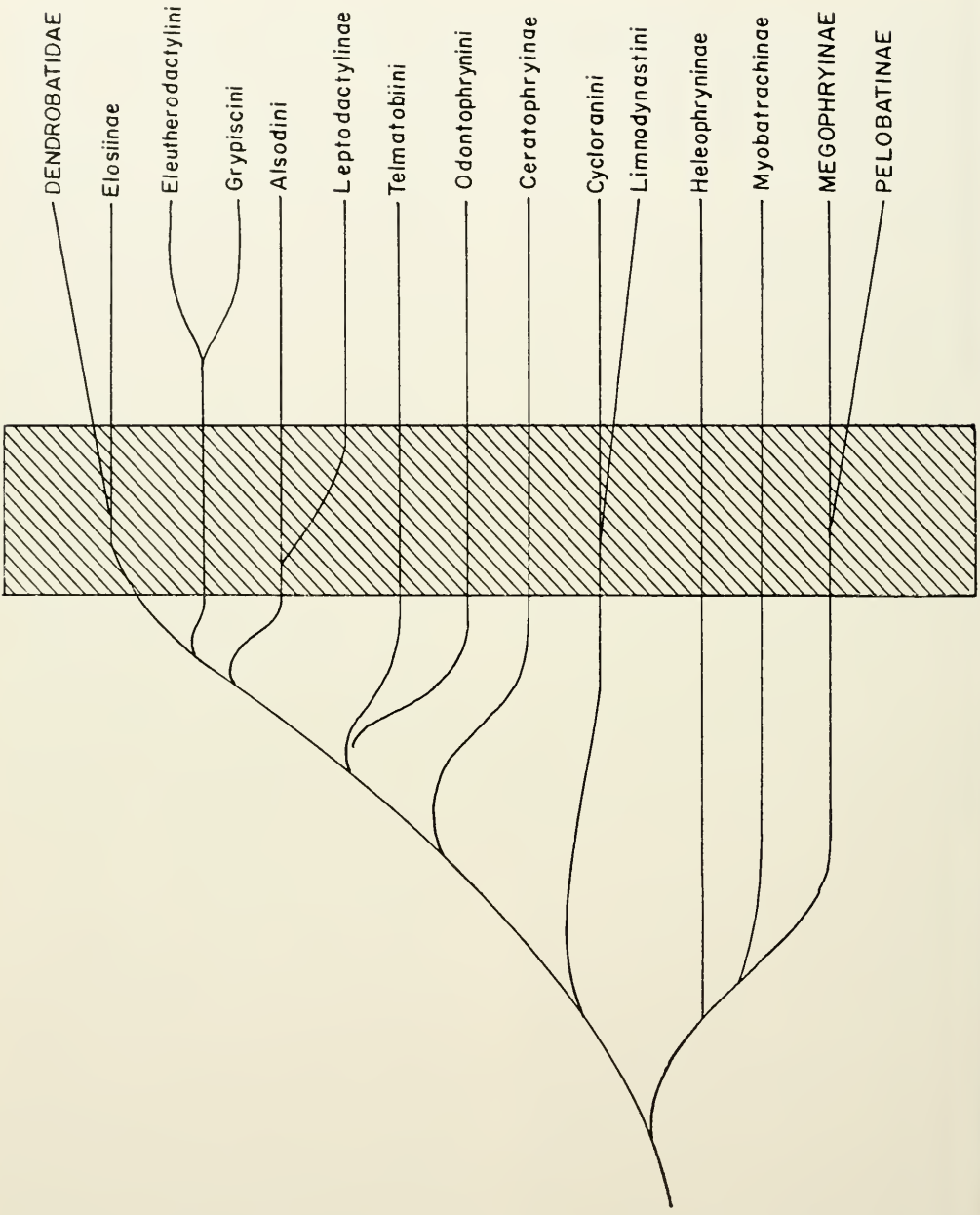

FIGURE 127. Dendrogram illustrating proposed relationships of the leptodactylid subfamilies and tribes and derived families. The hatched zone is Cretaceous time during which decreasing equability occurred. The vertical scale is not intended to indicate the duration or age of any group.

Neotropical subfamilies than is the Limnodynastini which are more specialized than the Cycloranini.

I consider each of the three subfamilies discussed above to have evolved independently from a megophryine ancestor. One could therefore argue that the Leptodactylidae are polyphyletic. The Cycloraninae appear to be ancestral to the Neotropical leptodactylids, but the Heleophryninae and Myobatrachinae are apparently not involved in the phylogeny

of the Neotropical leptodactylids. As stressed above, the Megophryinae and Australo-Papuan leptodactylids are similar in most character complexes. Taken in combination, the Cycloraninae, Heleophryninae, and Myobatrachinae form an evolutionary grade between the Megophryinae and the Neotropical leptodactylids. However, I am reluctant to accord both the Heleophryninae and Myobatrachinae familial status and consider equally unrealistic the idea of considering either or both subfamilies of the Pelobatidae. The Myobatrachinae could be more reasonably distinguished familially from the Pelobatidae than could the Heleophryninae. From an evolutionary standpoint, the Heleophryninae are a relict of the Megophryine stock which gave rise to the Cycloraninae (see below, pp. 208-9). The Myobatrachinae probably evolved from a contemporaneous megophryine. Whether this megophryine was subfamilially distinct from the group which gave rise to the Cycloraninae cannot be known in the absence of fossils. I doubt that these two megophryines were subfamilially distinct and therefore consider the Leptodactylidae monophyletic following the reasoning of Simpson (1961:124).

The subfamilies discussed below seem to have a common ancestry within the Leptodactylidae. This common ancestor was probably a cycloranine which was not unlike the modern Cycloranini.

The subfamily Ceratophryinae contains only two extant genera and is a morphologically isolated group. This isolation has been described by several workers who consider the subfamily to be a family more closely allied to the Bufonidae than to the Leptodactylidae (Cei, Limeses, Reig). In spite of the morphological isolation of the Ceratophryinae there are some striking similarities between the Ceratophryinae and the Odontophrynini. Boulenger (1882), Cochran (1955), Reig (1960b), Reig and Cei (1963), and Reig and Limeses (1963) suggested that *Odontophrynus* and *Stombus auctorum (=Proceratophrys)* are very closely related to the ceratophryines. The Odontophrynini may have been derived from a ceratophryine ancestor, but the extant odontophrynine genera exhibit fewer primitive characters than do the genera of the Telmatobiini. The Odontophrynini represent either the first or second divergence from the original stock of the Telmatobiinae. The Ceratophryinae seem to represent the earliest divergence from the Neotropical leptodactylid stock.

The remainder of the early Neotropical leptodactylid stock (after the Ceratophryinae diverged) is represented by the Telmatobiinae and derived subfamilies (Elosiinae and Leptodactylinae). Some of the terrestrial genera of the Telmatobiini resemble the primitive Australo-Papuan Cycloranini (Cycloraninae) but more closely resemble the other tribes of Telmatobiinae.

The Leptodactylinae are derived from the relatively primitive Alsodini *(Eupsophus).* The most primitive leptodactyline *(Pleurodema)* is very similar to *Eupsophus.* The two genera differ in the sternal apparatus, breeding biology, and loss of the quadratojugal. *Pleurodema* has an osseous sternal style (as do all other leptodactylines) and lays its eggs in a foam nest (like several other leptodactylines); these two characters clearly ally *Pleurodema* with the Leptodactylinae although its close relationship to *Eupsophus* is obvious and could be used to support the argument that the Leptodactylinae are only a tribe of the Telmatobiinae.

The Elosiinae are a small, morphologically homogeneous group except for the cranial adaptations of *Megaelosia.* The relationships of the subfamily to other leptodactylid groups are unclear and over-shadowed by the relationship between the Elosiinae and the Dendrobatidae. The Elosiinae exhibit many characters in common with the Alsodini, Grypiscini, and Eleutherodactylini, and I consider the elosiines to represent an early division from the alsodine stock which later gave rise to the Grypiscini and Eleutherodactylini.

I recognize two tribes in the Cycloraninae, the Cycloranini and the Limnodynastini. Of the two tribes, the Cycloranini are more primitive. The Limnodynastini are specialized in their breeding biology. None of the five limnodynastine genera has vertical pupils and all have free intervertebral discs, the cervical fused to the second vertebrae, and relatively long transverse processes of the posterior presacral vertebrae. *Adelotus brevis* and one species of *Limnodynastes* have outer metatarsal tubercles, which are otherwise lacking in the tribe. The foam-nesting habits and the modifications of the fingers in females of the Limnodynastini are considered adequate reasons for separating these five genera from the Cycloranini which do not lay their eggs in foam nests (except *Heleioporus*) and do not have finger fringes in the females. The foam-nesting habit of *Heleioporus* is quite different from that of the Limnodynastini but similar to that exhibited by the frogs of the *Leptodactylus fuscus* group. *Heleioporus, Neobatrachus,* and *Notaden* are closely related. Although their skeletons are similar, the three genera differ in breeding biology and some external characters. *Cyclorana* and *Mixophyes* differ from *Heleioporus, Neobatrachus,* and *Notaden* in many features of the skull and vertebral column, but do not closely resemble each other. They are derived genera but probably have evolved several characters in a parallel fashion (ankylosis of intervertebral discs to centra, separation of cervical and second vertebrae in adults, long transverse processes on the posterior presacral vertebrae, and lack of a frontoparietal fontanelle). The last character may be primitive to the presence of a fontanelle, but in the leptodactylid groups the primitive genera frequently have a frontoparietal fontanelle.

The Ceratophryinae and Heleophryninae do not exhibit a great amount of intrasubfamilial variability in that they are small groups. The Myobatrachinae are morphologically homogeneous in many characters but are heterogeneous in many others. With the possible exception of bufonid and ranoid derivatives (see below), the myobatrachines do not figure prominently in bufonoid evolution. With respect to the Leptodactydae, the Myobatrachinae are an evolutionary dead-end.

The Ceratophryinae and Telmatobiinae apparently evolved from cycloranine ancestors. The Ceratophryinae represent an early divergence of the Neotropical stock and are a morphologically isolated and small group. The Telmatobiinae are a morphologically diverse and large group with one fossil and 24 Recent genera. I divide the Telmatobiinae into five tribes. The Telmatobiini (5 genera) and Odontophrynini (2 genera) are the most primitive tribes and the Alsodini are but slightly more advanced. The former two tribes have apparently not given rise to additional groups and have the bulk of their species in temperate or Andean South America. The Odontophrynini share several characteristics with the Ceratophryinae and may be early derivatives of that group which have paralleled the Telmatobiini. At present, I include the odontophrynines in the Telmatobiinae because they lack the distinctive vertebral column and vertebral shield of the ceratophryines. Cei (1965) demonstrated that the skin proteins of *Ceratophrys* and *Lepidobatrachus* set these genera off from the other leptodactylids including *Odontophrynus* and *Proceratophrys*. The distinctive ilia of the ceratophryines are identical with those of the odontophrynines and unlike those of all other leptodactylids. The solution of the problem of whether the odontophrynines represent a proto-ceratophryine or a telmatobiine stock will probably require some fossil data.

The Alsodini and their derivatives make up the majority of the Neotropical Leptodactylidae. The Alsodini occur in temperate and Andean South America, with one genus *(Thoropa)* endemic to southeastern Brasil. The tribe is somewhat heterogeneous in that two of the

genera *(Eupsophus* and *Hylorina)* have a type II cervical cotylar arrangement and lay relatively numerous small eggs in aquatic situations. Both of these genera engage in axillary amplexus and have outer metatarsal tubercles. One of them *(Hylorina)* has vertical pupils. The other two alsodine genera *(Batrachyla* and *Thoropa)* have a type I cervical cotylar arrangement and lay relatively few large eggs in moist terrestrial situations. The larvae of both genera become aquatic after the nest is inundated. Both genera have outer metatarsal tubercles and horizontal pupils. *Batrachyla* engages in inguinal amplexus (Barrio, 1967a), but amplectic behavior has not been observed for *Thoropa.* As mentioned above, the Leptodactylinae seem to have been evolved from an ancestral stock with the characteristics of *Eupsophus. Batrachyla* and *Thoropa* are probably representative of the alsodine stock which gave rise to the Eleutherodactylini, Grypiscini, and Elosiinae. I consider the Elosiinae to represent an early divergence from this stock because the Elosiinae have aquatic larvae. Osteologically, the Elosiinae are isolated from the Grypiscini and Eleutherodactylini. I consider the Grypiscini more primitive than the Eleutherodactylini. The eggs of grypiscine genera are large and deposited in moist terrestrial situations as is the case in the Alsodini, but in contrast to the Alsodini, the larvae are not aquatic (Lutz, 1944). The eleutherodactyline genera exhibit direct development. Unlike the grypiscine larvae, eleutherodactyline larvae never free themselves from the enclosing egg envelopes. The Grypiscini make up a small group which is restricted in distribution to the coastal ranges of southeastern and southern Brasil. The Eleutherodactylini range over the entire tropical and subtropical zones of the Americas except in the arid regions of Central America, Ecuador, Peru, and Venezuela. The zenith of the Leptodactylidae is *Eleutherodactylus* which contains probably 400 species and occurs over most of the range of the Eleutherodactylini. Direct development is probably the single adaptive change made by this tribe which permitted the tribe to evolve into such a large group. The success of the genus *Eleutherodactylus* is measured by its diversity and adaptability. The genus is rich in species throughout the West Indies and occurs in semiarid as well as very moist habitats. Unlike many leptodactylid genera, it is not restricted to lowland situations where there are ponds (a requirement for species with aquatic larvae) but ranges altitudinally to at least 4200 meters in the Andes.

EXTRAFAMILIAL RELATIONSHIPS OF THE LEPTODACTYLIDAE

I have discussed the relationships between the Pelobatidae and Leptodactylidae and the relationships within the Leptodactylidae above. In some cases, reference was made to the close relationship between a leptodactylid group and the frogs of other families. I consider the close relationship between the Pelobatidae and Leptodactylidae to be established, and also consider the statement "the Leptodactylidae are the stem bufonoid group" to be established. If the Leptodactylidae are the stem bufonoid group, then all other bufonoid families are leptodactylid derivatives or are independently derived from a pelobatid stock. The works of Griffiths (1963), Inger (1967), Kluge and Farris (1969), Noble (1922, 1931), and Tihen (1965) have clearly established that the archaic frog families (Ascaphidae, Discoglossidae, Pipidae, and Rhinophrynidae) did not directly give rise to the "advanced frogs."

These authors agree that these four families are clearly primitive and that the other frog families are advanced. Most consider the Pelobatidae to bridge the gap between "primitive" and "advanced" frogs. There is considerable debate as to whether the Microhylidae are primitive or advanced frogs. The proponents of the primitive position (Hecht, 1963, Inger,

1967, Orton, 1957, and Starrett, 1968) based much of their argument on the tadpole morphology, whereas the advocates of the advanced, ranoid position (Griffiths, 1963, Noble, 1922, 1931, and Parker, 1934) rely on the pectoral architecture, thigh musculature, and the variable sacral-presacral central articulation. Further discussion of the relationships of the Microhylidae is withheld pending new data and perhaps another monograph of the family. I have plotted values for some of the microhylid subfamilies in the figure illustrating the degree of primitiveness in frog groups (Fig. 126). The subfamily Microhylinae appears to be the most primitive subfamily of this group on the basis of the characters I used. Relatively little data of the breeding biologies of microhylids are available, and I have seen relatively few genera in computing my values of primitiveness for the family. In general the values are in agreement with the idea of the phylogeny of microhylids advanced by Parker (1934) —that the group represents an early ranid divergence. The data are not in accord with the position taken by Hecht (1963) and Starrett (1968)—that the family represents one of the archaic families. The remaining frog families seem to have some relationship to the varied leptodactylid stocks.

I consider the rhinodermatids to represent a Neotropical bufonid derivative and therefore include that genus in a discussion of the relationships of the Bufonidae to the Leptodactylidae. As mentioned above, among the extant leptodactylid groups the Myobatrachinae are most like the Bufonidae and are presumably the modern representatives of the proto-bufonid stock. The two groups agree strikingly in the structure of the tadpole mouthparts. All bufonids (and *Rhinoderma*) lack teeth; few leptodactylids are edentate, but this character-state is most pronounced in the Myobatrachinae. All bufonids and myobatrachines have dilated sacral diapophyses. Myobatrachines have a type I cervical cotylar arrangement (type II in bufonids), free intervertebral discs (procoelous vertebrae in bufonids), and lack Bidder's organ (present in bufonids). Most bufonids lack a prezonal element in the pectoral girdle (omosternum present in *Nectophrynoides* and at least one *Bufo, B. haematiticus),* whereas most leptodactylids have a large omosternum and manubrium. The prezonal element in myobatrachines is small in most genera and absent in some. Although the Neotropical bufonids have radiated (7 endemic genera), there is no close relationship between the Neotropical bufonids and leptodactylids.

The relationships of the Centrolenidae are not apparent. Before the significance of the intercalary cartilage was accepted, they were often placed in the Hylidae or Leptodactylidae. Centrolenids are arboreal, have aquatic tadpoles, intercalary cartilages, T-shaped terminal phalanges, the astragulus and calcaneum fused, and lack a prezonal element in the pectoral girdle. Most authors consider them hylid derivatives (Eaton, 1958). Much of the argument that centrolenids are hylid derivatives rests on a conviction that all Neotropical taxa with intercalary cartilages are related. The hyolarynx of *Centrolenella* is distinctive (figured by Eaton, 1958) and quite different from that of most bufonoid genera. The variation in the hyolarynx of hylids has not been adequately investigated and until it has, the taxonomic value of the distinctive hyolarynx of *Centrolenella* remains unknown.

The Dendrobatidae are an elosiine leptodactylid derivative and not ranoid as claimed by Griffiths (1959, 1963). This point was discussed in greater detail in the section of the Elosiinae (pp. 163-4). Griffiths (1963), in arguing in support of his contention that the Dendrobatidae are a subfamily of the Ranidae, cited the apparent parallelisms in the Petropedetinae (African ranids). My study of the group is limited to some dissection and examination of cleared and stained individuals but results in the conclusion that the two groups exhibit considerable

similarity in myology and osteology. The similarities are quite striking and probably reflect a community of ancestry rather than parallelism. However, it should be borne in mind that I have not studied the other ranid subfamilies and genera in detail and cannot therefore convincingly argue that the similarities are not due to parallelism.

The relationships of the Hylidae are not apparent, but the family is usually tacitly considered a leptodactylid derivative. Inger's (1967:Fig. 6) phylogeny suggests that the Hylidae are the sister group (*sensu* Hennig) of the Ranidae + Rhacophoridae. The suggestion is unique and mentally provocative but needs further investigation. Previous authors were committed to placing the Hylidae and Ranidae in different suborders because of convictions that the pectoral architecture or sacral centrum were characteristic of basic dichotomies. The same convictions required the Microhylidae to be closely related to ranids.

The Pseudidae were considered leptodactylids until Parker (1935) suggested that they were hylids (because of the presence of an intercalary phalanx). The intercalary phalanx of pseudids is elongate and osseous instead of short, disc-like, and cartilaginous as in centrolenids, hylids, hyperoliids, rhacophorine ranids, and some microhylids *(Phrynomerus)*. Savage and Carvalho (1953) named a new family for the Pseudidae *(Lysapsus* and *Pseudis)* because they considered the accessory phalanx analogous to the intercalated cartilage. As pointed out by Burger (1954), Savage and Carvalho's "new family" was authored by Fitzinger (1843). Savage and Carvalho (1953) considered *Pseudis* more primitive than *Lysapsus* and suggested that the family was derived from the Leptodactylidae. Burger (1954) considered *Lysapsus* more primitive than *Pseudis* and suggested that the group was a hylid subfamily. I have not studied pseudids in detail, and much information is lacking for *Lysapsus*, but I consider the group more closely allied to leptodactylids than to hylids. The pseudids are not closely related to any leptodactylid group.

The ranoid families (Hyperoliidae, Sooglossidae, Ranidae, and Rhacophoridae) are usually considered remote from leptodactylids. *Sooglossus* and *Nesomantis* were included in the Sooglossinae, a pelobatid subfamily with ranoid parallelisms by Noble (1931). The subfamily is restricted to the Seychelles. Darlington (1957) doubted on zoogeographic grounds (with preconceived acceptance of Matthew's conclusions) that the Sooglossinae could be pelobatids, and Griffiths (1960), with similar zoogeographic biases, demonstrated ranoid affinities for the group and elevated the subfamily to family rank. The Sooglossidae have some pelobatid, myobatrachine leptodactylid, and ranoid traits and are conceivably modern representatives of a leptodactylid derivative that gave rise to the Ranidae. Until further study is made of the numerous hyperoliid, ranid, and rhacophorid genera, additional comments on the relationships of these families to leptodactylids are held in abeyance. Vertical pupils are considered to be primitive by me and vertical pupils do not occur in the Ranidae or Sooglossidae. Vertical pupils are common in the genera of two of the subfamilies of Laurent's (1951) Hyperoliidae (Astylosterinae and Hyperoliinae). Most of these genera also lack outer metatarsal tubercles.

ZOOGEOGRAPHY

Almost without exception, previous zoogeographic studies utilizing or involving anurans have been Matthewian in analysis and conclusion. Darlington (1957) voiced numerous suggestions concerning anuran zoogeography but lacked an understanding of the relationships of most groups. Noble (1924, 1926c, 1930) attacked many zoogeographic enigmas, but his approach was strictly Matthew-

ian. Many macrosystematic problems of frogs have been studied and solved in the past decade, and the major evolutionary patterns of the Anura are only now beginning to emerge. Many problems, principally minor ones, remain to be solved; a major difficulty to be overcome is the relationships of the families assigned to the Ranoidea, especially the Microhylidae. Paleontological work has continued to force biologists to accept the antiquity of frogs; the order had diversified into several families by the Jurassic (Tihen, 1965). As the known antiquity of frogs increases, so must the consideration that continental drift may have played an important role in establishing their present distributions. However, simply because a group is an old one, continental drift need not be invoked to explain distribution patterns (cf. Kluge, 1967).

The present distribution of the Leptodactylidae (Fig. 1) is suggestive of a southern origin and dispersal. No fossil evidence is available to establish the presence of the family in the northern hemisphere before the late Tertiary except for the Lower Eocene *Indobatrachus* from peninsular India. Noble (1930) and Darlington (1957) cited the fossil as evidence of a northern occurrence of the otherwise Australo-Papuan Myobatrachinae. Both authors assumed that peninsular India has always been part of the Asian continent or at least has been part of it for sufficiently long that, zoogeographically, India is part of Asia. However, contrary evidence is impressive. Paleomagnetic studies place Bombay at 40° S in the Jurassic and record a steady northerly movement of the subcontinent throughout the later Mesozoic and Cenozoic. During the Eocene, Bombay was at 10° S (Takeuchi, Uyeda, and Kanamori, 1967), or at about the level of northern Australia, and the present Himalayan region was crossed by the Sea of Tethys.

The frogs of the family Leptodactylidae presently occur in Australia (and New Guinea and Tasmania), in southern Africa, and in the Neotropics from southern Chile and Argentina (53-54° S) north to Arizona, Florida, New Mexico, and Texas (30-33° N). With the exceptions of a few leptodactyline and telmatobiine genera which range northward into Middle America and the southern United States, no leptodactylid subfamily occurs on two continents. The Cycloraninae and Myobatrachinae occur only in the Australo-Papuan Region (two genera reach eastern New Guinea and three reach Tasmania), the Heleophryninae (monotypic) occur only in southern Africa, and the Ceratophryinae, Elosiinae, Leptodactylinae, and Telmatobiinae occur only in South and Middle America. With the exception of *Indobatrachus*, the fossil record for each subfamily (insofar as it is known) is included in the Recent distribution of the group (on the same continent). Five genera of the Telmatobiinae range outside of South America; four of these (*Hylactophryne*, *Sminthillus*, *Syrrhophus*, and *Tomodactylus*) do not occur in South America, but the other (*Eleutherodactylus*) is wide-spread in tropical South America. *Sminthillus* is a Cuban endemic, and the other three non-South American genera are principally distributed on or around the Mexican Plateau. Three genera of the Leptodactylinae range outside of South America. *Pleurodema* occurs in the savannas of central Panamá but has its center of distribution in temperate South America. *Physalaemus* occurs in the Central American lowlands as far northwest as Oaxaca and Veracruz, México, but has its center of distribution in subtropical and tropical Argentina and Brasil. In the case of both genera, only a single species enters Central America. *Leptodactylus* ranges northwestward through Central America to Texas and Sinaloa but all Central American species are also found in northern South America. *Leptodactylus* also occurs on Hispaniola and Puerto Rico and on several islands in the Lesser Antilles, but is not represented by extra-South American endemics. All of the Middle American leptodactylines are

South American species which have spread northward since the Late Pliocene closure of the Panamanian portal (Lloyd, 1963). The Telmatobiine genera all belong to the Eleutherodactylini. Three of the extra-South American genera *(Sminthillus, Syrrhophus,* and *Tomodactylus)* are derivatives of the alpha division of *Eleutherodactylus.* The alpha division of *Eleutherodactylus* is centered in the West Indies (about 100 species) but also occurs in the Andean system in Colombia, Ecuador, Guyana, and Venezuela. The fourth extra-South American eleutherodactyline *(Hylactophryne)* is not obviously derived from *Eleutherodactylus* and shows a greater affinity with an Amazonian genus *(Ischnocnema).* The paleogeographic maps compiled by Harrington (1962), Jacobs *et al* (1963), and especially Lloyd (1963) strongly suggest that South America was not connected to North America during the Mesozoic and most of the Tertiary. Contact was established in the Pliocene (Lloyd, 1963). Animals could have moved northward across the volcanic island chain in the latter half of the Tertiary but the degree of isolation of animal groups suggests that the terrestrial South American fauna was isolated in South America until the Pliocene. No leptodactylid group reached North America via a Panamá-Costa Rica route until late in the Tertiary. Some leptodactylids may have reached North America earlier (perhaps Miocene) by way of the Antillean arc. Therefore, until the Middle Tertiary we may ignore North America insofar as leptodactylids are concerned. The history of the family lies in South America and the southern hemisphere. Vinson and Brineman (1963) suggested that Middle and South America were connected by a Late Paleocene land bridge. These authors argued that this is true because of the lack of Danian-Paleocene marine formations in the Isthmian region of Panamá. This land bridge was essential to Savage's (1966), analysis of the history of the Middle American herpetofauna.

The Australo-Papuan and African leptodactylid groups share a few characters but each of the three groups has more characters in common with the pelobatid subfamily Megophryinae. The Megophryinae seem to be ancestral to the Leptodactylidae, and the lack of obvious interrelationships between the Heleophryninae, Cycloraninae, and Myobatrachinae suggests that each subfamily is an independent derivative of the megophryine stock. The Cycloraninae and Heleophryninae share one interesting character (the fusion of the cervical and second vertebrae) which does not appear elsewhere in the family. The fusion appears in some African and South American bufonid genera, rhinodermatids, palaeobatrachids, and pelodytids; the significance of this character distribution is not entirely apparent at present.

The Recent distribution of the Megophryinae is much smaller than its early Tertiary distribution. *Eopelobates* is known from Europe in the early Miocene and western North America in the Eocene and Oligocene and is probably represented in the late Cretaceous deposits of Wyoming. The Megophryinae are presently restricted to southeastern Asia and the Indo-Australian archipelago west of Wallace's Line but do not occur on Luzon and Masbate (Philippines).

Both the Cycloraninae *(Lechriodus)* and Myobatrachinae *(Crinia)* occur in eastern New Guinea, and *Lechriodus* also occurs on the Aru Islands. *Lechriodus* has three endemic species in New Guinea and the Aru Islands, but one other species also occurs in eastern Australia. The single *Crinia* which occurs on New Guinea is also widespread on the Australian mainland. Each subfamily is distributed over most suitable anuran habitat on the Australian mainland and both are absent over most of the western Eyrean desert.

Among living leptodactylids, the Cycloranini are least unlike the primitive Neotropical leptodactylid genera. The morphological hiatus between the Neotropical leptodactylids and the several pelobatid stocks requires an intermediate

stage whose characteristics are like those exhibited by the Cycloranini. Darlington (1957, 1965) considered the temperate South American frog fauna depauperate and thus of little zoogeographic importance. Cei (1962a) and Vellard (1957) contended that the fauna is relict. Vuilleumier (1968) analyzed the amphibian fauna of the *Nothofagus* forests of temperate South America and noted that the present anuran distributional patterns are a result of Pleistocene events but admitted that the high degree of endemism is a consequence of a long history in the Patagonian forests. Vuilleumier (1968) considered the frog fauna of the *Nothofagus* forests to consist of four elements: 1) leptodactylid stocks which are autochthonous and have not subsequently diversified; 2) autochthonous leptodactylid elements which have subsequently radiated into northern South America; 3) *Nothofagus* endemics which are derived from tropical South American leptodactylids; and 4) bufonid and leptodactylid stocks which are widespread in South America and have more species outside of the *Nothofagus* forests than in it. He considered the available data as inadequate to permit determination of whether these groups are secondary or primary inhabitants of southern South America. Vuilleumier's analysis must be rejected because his conclusions are in part based upon the erroneous conclusions of other authors. His second element [2), above] consisted of *Eupsophus*. As I pointed out (Lynch, 1971), *Eupsophus* (as used by Vuilleumier and many other authors) is a composite of seven genera. *Eupsophus* is restricted to western Argentina and Chile, except for two Andean species in southern and central Peru. Vuilleumier's third element has been altered taxonomically by Barrio (1967a) and Lynch (1971). *Batrachyla* is valid and contains three species (all *Nothofagus* endemics); the genus is not an *Eleutherodactylus* derivative but an offshoot of a *Eupsophus-Hylorina* stock. The fourth element of Vuilleumier was misrepresented in part. Vuilleumier included the genera *Bufo* and *Pleurodema*. The former is widespread and species-rich in tropical and subtropical South America but *Pleurodema* is basically a temperate South American genus (defined on the basis of cool or cold winters and cool summers). The distributions of eight of the ten species of the genus are contained in temperate South America; the other two species range northward into subtropical and tropical areas in Brasil, Colombia, Venezuela, and the Guianas (Fig. 128). *Pleurodema* is a temperate zone genus which has invaded the tropical zone, whereas *Bufo* is more a tropical zone genus which enters the temperate zone.

Batrachophrynus, Batrachyla, Caudiverbera, Eupsophus, Hylorina, Pleurodema, Telmatobufo, and *Telmatobius* are temperate South American leptodactylid genera either wholly or principally restricted to the temperate zone. This list of genera includes most of the primitive Telmatobiinae and the most primitive living Leptodactylinae. *Ceratophrys, Lepidobatrachus, Limnomedusa,* and *Thoropa* are also considered primitive, and with the exception of *Ceratophrys* do not range north of the southern subtropical zone.

The primitive Cycloranini morphologically resemble the primitive Neotropical genera, which are the principally temperate South American genera. These coincidences require that we regard the similarities as convergent or that we consider them products of common ancestry. The latter conclusion further requires some land connection between Patagonia and Australia; the most plausible route is via Antarctica. To conclude that the route involved the Holarctic Region requires a massive extinction of the stocks which passed through the Holarctic and Neotropical regions, and further requires that these stocks survived only in temperate South America from which they gave rise to new groups which then invaded the tropical zone. A possible causative agent for such a mass extinction would be climatic zonation and decreas-

FIGURE 128. Distribution of leptodactylids in South America. (A) Black areas encompass the range of the Alsodini. *Thoropa* is restricted to southeastern Brasil. The dotted line encloses the range of the genera *Telmatobius* and *Batrachophrynus*. Two other genera of the tribe *(Caudiverbera* and *Telmatobufo)* occur in the black area in Chile. (B) Ranges of the genera *Limnomedusa* and *Plevrodema,* the most primitive genera of the Leptodactylinae. (C) Range of the Elosiinae. The area in southeastern Brasil encompasses the distribution of *Crossodactylus* and *Megaelosia;* the genus *Hylodes* also occurs on Cerro Duida, Amazonas, Venezuela. The range of the Elosiinae in southeastern Brasil approximates the range of the Grypiscini.

ing climatic equability of the northern hemisphere during Cretaceous time. However, this explanation results in two principle difficulties: 1) why did not leptodactylid stocks survive in areas in the northern hemisphere which retain high equabilities?, and 2) the megophryine pelobatids are probably equally sensitive to low equabilities yet they persisted in North America until the Oligocene and survive today in southeast Asia.

Equability is a property of climate which expresses departures from 14.0° C and thus responds primarily to temperature extremes (Axelrod and Bailey, 1968). High equabilities reflect little variation in temperatures about an annual mean of 14.0° C. Equability applies equally well to warm and cold regions. Bailey (1960, 1964) also noted a second aspect of temperature that affects biotic composition —effective temperature, which expresses warmth of the climate in terms of temperature and the duration of the summer (Axelrod and Bailey, 1968). Effective temperature is independent of the mean annual range of temperatures.

Axelrod and Bailey (1968) noted that many areas in the southern hemisphere harbor relicts of the Cretaceous flora (cycads, tree ferns, podocarps, araucarias). It is in some of these regions (south Africa, Australia, southern South America, southeastern Brasil) that primitive leptodactylids (Cycloraninae, Myobatrachinae, Heleophryninae, Telmatobiini, and Alsodini) occur. These areas are characterized by high climatic equability (M = 60+).

Mesozoic climates were characterized by high equabilities (Axelrod and Bailey, 1968). Equability is increased if the locality is associated with large bodies of water (for example, the equability of localities along the Peruvian coast is higher than might be expected, as are the equabilities for localities in coastal Uruguay). The broad marine embayments and epeiric seas of Mesozoic landmasses probably contributed to the maintenance of high equabilities in continental situations. Under a temperature regime of high equabilities, the dispersal routes of Mesozoic animals would not be temperature-limited. The southern hemi-

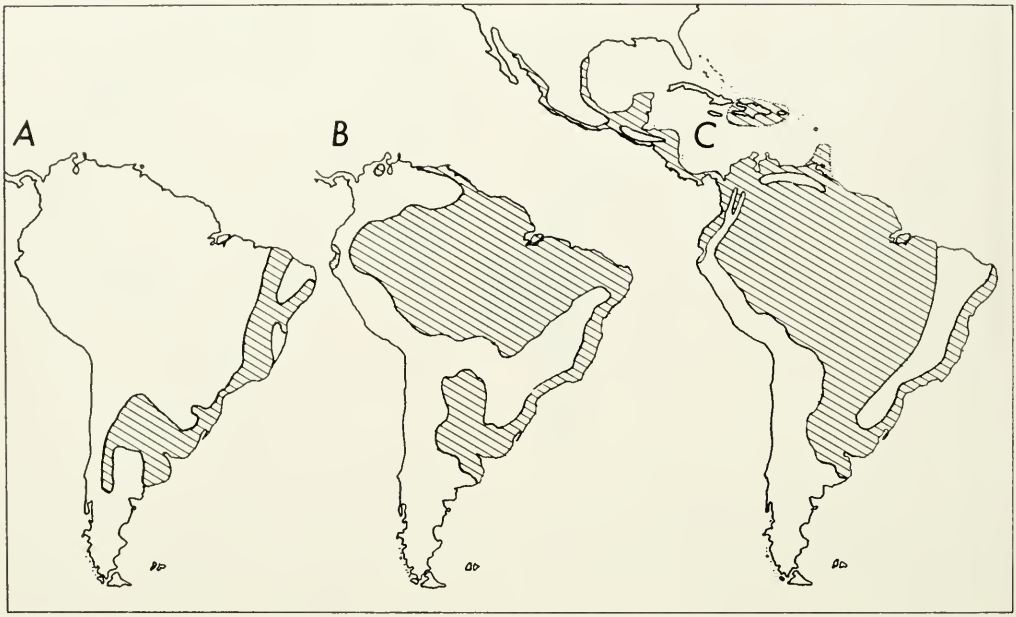

FIGURE 129. (A) Distribution of the Odontophrynini. (B) Distribution of the Ceratophryinae. (C) Distribution of the Leptodactylinae except for the primitive genera *Limnomedusa* and *Pleurodema*.

sphere leptodactylid stocks could have invaded the northern hemisphere were land connections available because the northern hemisphere was also under a regime of high equabilities until the Cretaceous. During the Cretaceous many plant and animal groups became extinct or began to flourish. At the same time the earth began to experience a marked climatic zonation. With the development of climatic zonation, broad areas of the world experienced a decrease in equability. Axelrod and Bailey suggested that the primitive faunas and floras presently living in areas of high equability survived in those regions because these groups are, and their ancestors were, adapted to climates of high equability.

The part of South America (Figs. 129-130) with high equabilities (58+) includes the ranges of almost all of the primitive genera of leptodactylids *(Batrachophrynus, Batrachyla, Caudiverbera, Eupsophus, Hylorina, Lepidobatrachus, Limnomedusa, Pleurodema, Telmatobius,* and *Telmatobufo).* A few of the species in these genera occur in areas of low equability (for example, *Pleurodema brachyops* and *P. diplolistris* occur in areas with equabilities of 40-45). The Leptodactylinae probably evolved in response to the decreasing equability of the Late Cretaceous (see below). Before returning to the history of the Leptodactylidae in South America, it is convenient to review briefly the history of the African and Australo-Papuan groups and the Megophryinae and to discuss the possible role of climatic equability in the establishment of the Recent distributions of these groups.

The Megophryinae have survived in areas with relatively high equabilities. Even the temperate eastern Himalayas have equabilities of 60+. Regardless of which stance (Wegenerian or fixed continents) one wishes to take, the Megophryinae are probably a group which evolved in the northern hemisphere. The Cycloraninae, Heleophryninae, Myobatrachinae, and Pelobatinae are the derivatives of the Megophryinae. Two of these derivatives are Australo-Papuan, one south African, and one Holarctic. The proximity of the present distributions of the Megophryinae, Cycloraninae, and

Myobatrachinae tempts one to assume that megophryine stocks crossed the Indo-Australian archipelago into Australia in the early Cretaceous with the Marsupalia and boid and elapid snakes. However, Inger (1954) considered the Megophryinae late invaders of the Philippine Islands. Of further significance in this regard is the wider distribution of the Megophryinae in the Late Cretaceous and early Tertiary of North America and Europe. Proponents of continental drift argue that the proximity of the Sundan shelf and Sahul shelf is a relatively recent phenomenon. The Indo-Australian archipelago is usually cited as the route whereby northern-evolved groups reached Australia in the Cretaceous (Clemens, 1968, Darlington, 1957, 1965). Biologists seeking support for this route have cited Audley-Charles (1966), who after studying the geology of Timor concluded that the relationship between Timor and the Sahul shelf has not changed since the Middle Triassic and that the relationship between Timor and

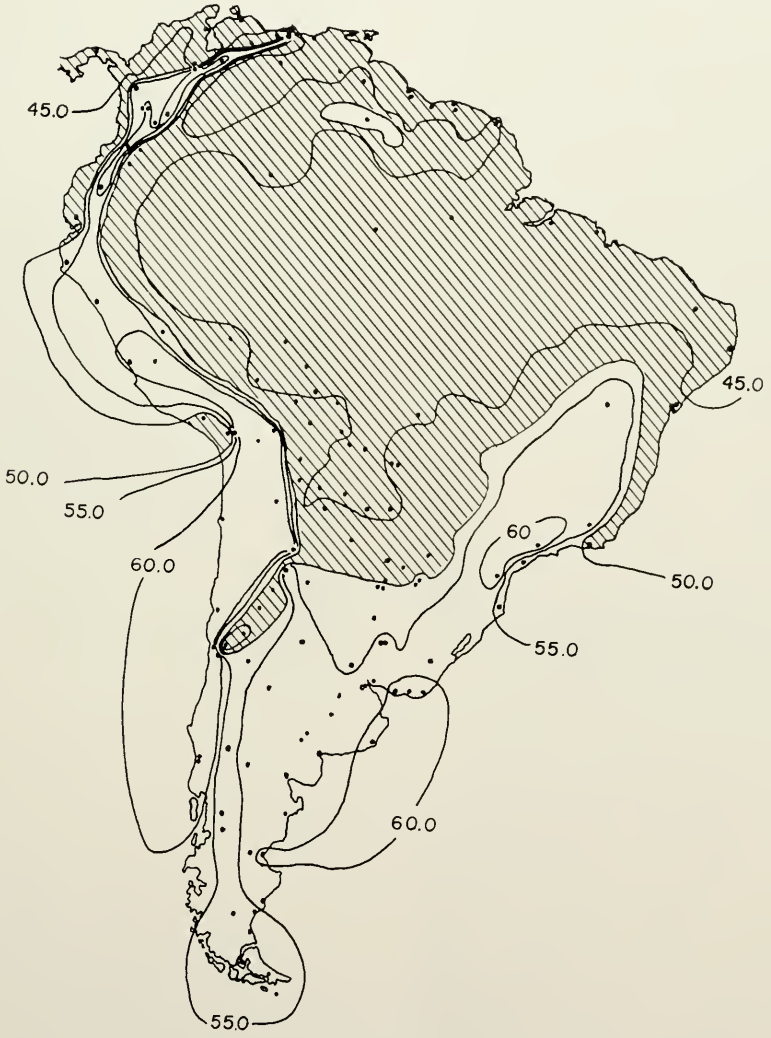

FIGURE 130. Map of South America with isoequaphane lines (45, 50, 55, 60 and above) superimposed. All dots on the map represent stations for which equability values (after Axelrod and Bailey, 1968) were computed. The hatched areas have equabilities of 50 or less.

the rest of the archipelago is apparently as ancient. As Hallam (1967) remarked, ". . . something more than island chain links is required to account for the presence in Australia of the lungfish *Neoceratodus* and large Jurassic and Cretaceous dinosaurs."

A Jurassic dispersal of megophryine stocks through eastern Africa onto peninsular India, Antarctica, and Australia (Fig. 131) would explain the similarities of the Heleophryninae and some primitive Cycloranini, but would require that these continental masses be in close proximity instead of being widely separated as they are today. This route also requires that the megophryines not invade South America which was in close proximity with Africa until the Neocomian (Lower Cretaceous). The megophryine stock probably had the same reproductive biology as do the living pelobatids and the Australo-Papuan leptodactylids. During the Jurassic and early Cretaceous, the Brasilian and Guiana shields must have been formidable barriers to pond-breeding frogs. On the slopes of these uplifted shields, ponds would be rare if they existed at all. In contrast, ponds would be available along the western edge of Africa in the vicinity of the East African Gulf of Tethys sea (Hallam, 1967). If the interior of Antarctica was as forbidding to amphibians as Darlington (1965) reasons it must have been, then the only southern route would have been across that part of Antarctica now called Enderby Land and the American Highland. Hallam (1967) suggested that a deep marine sea separated South America and Africa from Antarctica, Australia, and Peninsular India in the Neocomian. Harrington (1962) noted the occurrence of marine facies over the southernmost tip of South America in the Neocomian but the extent of this marine sea was not as great as suggested by Hallam. The leptodactylid stock that did reach southern South America probably entered the continent in Callovian (Upper Jurassic) or Neocomian (Lower Cretaceous) times. Whether dispersal was by a corridor or filter bridge (Darlington, 1957) route is non-consequential; dispersal could even have been via a sweepstakes route. The significant point to be made here is that contrary to Darlington's (1965:38) assertion, one group of terrestrial vertebrates (leptodactylid frogs) does show special relationships between the southern temperate forms on different continents. Darlington stressed the absence of closely related cold-temperate vertebrates in Tierra del Fuego and Tasmania. However, this absence is explained by increased cold and lowered equabilities in Tierra del Fuego. Once the Australo-Papuan groups reached Peninsular India and Australia, and the Australo-Papuan Cycloranini spread across Antarctica to Patagonia, continental connections were no longer necessary because each of the subfamilies occupied the appropriate continental masses. The probable time period was [or perhaps somewhat earlier than] the Neocomian (Lower Cretaceous). After this time, Australia and South America appear to have been completely isolated from all other land masses until the middle Tertiary in the case of Australia (connection via the Indo-Australian archipelago) and the late Tertiary in the case of South America (connection via the Panamanian Isthmus).

The early Cretaceous continental separations were followed by the imposition of a severe climatic regime on the distribution of the early Cretaceous faunas and floras. Insofar as the Megophryinae and their derivatives are concerned, the development of this new climatic regime had several important consequences: 1) evolution of a low-equability adapted group, the Pelobatinae, in the northern hemisphere; 2) gradual extinction and range restriction of the Holarctic Megophryinae; 3) isolation of the Heleophryninae into a high equability area in south Africa and/or extinction of Heleophryninae or Megophryinae in east Africa; 4) extinction of Myobatrachinae in peninsular India; and 5) evolution of low-equability adapted groups in Australia and South America.

The high-equability adapted groups were restricted in geographic distribution to areas of high equability in southern South America and Australia. The development of climatic zonation probably resulted in physiological stresses on the

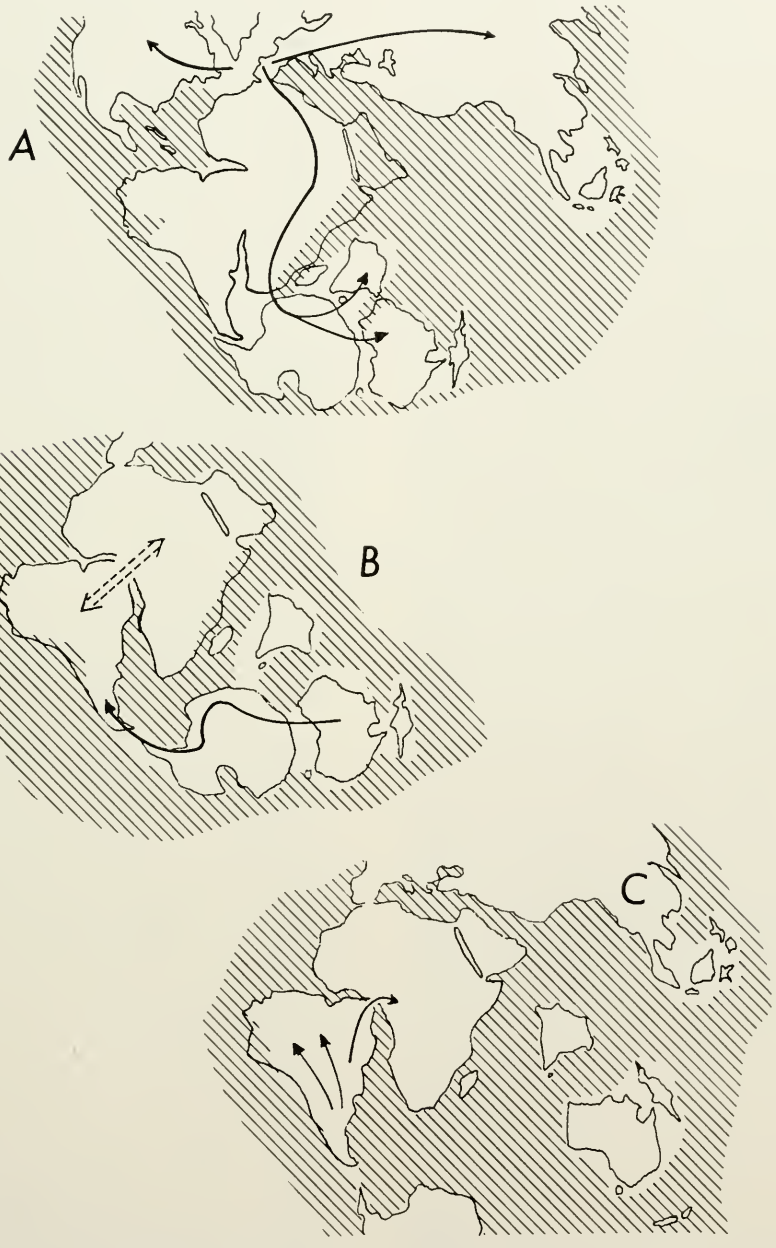

FIGURE 131. Paleozoogeographic maps for three stages of the evolution and dispersal of leptodactylid frogs and for related groups. (A) Jurassic (Callovian)—southerly dispersal of Megophryinae. (B) Late Jurassic or earliest Cretaceous—Africa is isolated from southern masses; climatic equability is beginning to influence dispersal routes. Leptodactylid invasion of South America. The dashed line is the route of free exchange of other vertebrate groups (e.g., characoid fishes and pipid frogs). (C) Middle Cretaceous—Africa-South American connection is tenuous, Neotropical leptodactylids are radiating from Patagonia into low-equability zones. Bufonidae spread into Africa.

surviving fauna and flora; these stresses forced a concentration of the Cretaceous genera into the remaining areas of high equability and may well have been the principle factors causing a radiation of the Neotropical leptodactylids. The development of foam-nesting habits in the breeding biologies of the Limnodynastini may have been stimulated by decreasing equability. The foam-nesting habit enables the frogs of this group to survive in more xeric, and less equable, climates than are suitable for the Cycloranini and Myobatrachinae.

The distribution of leptodactylids in South America was greatly restricted during the later Cretaceous, when climatic zonation was developing and equability was decreasing. The fauna probably included only a half dozen genera (*Batrachyla, Caudiverbera, Eupsophus, Lepidobatrachus, Telmatobufo* or *Neoprocoela,* and *Thoropa).* In response to decreasing equabilities the range of the Alsodini was contracted and probably resulted in the isolation of a relict population on the Brasilian shield. This population probably gave rise to the Elosiinae and Grypiscini. The decreasing equabilities also resulted in the evolution of a group of frogs utilizing foam-nests in their breeding biology. The ancestral stock of this group is *Eupsophus* which gave rise to *Pleurodema* and possibly to *Limnomedusa.* The presence of a foam-nest enabled these frogs to breed in more xeric environments, but presumably the adults were adapted to high equabilities and were therefore unable to successfully invade the tropical zone. New genera evolved to occupy this region (*Leptodactylus* and *Physalaemus). Batrachyla* and *Thoropa* lay their eggs in moist terrestrial situations but require water for their aquatic tadpoles. The Elosiinae represents a derivative of this group which became isolated on the Brasilian and Guiana shields (high equability). The Eleutherodactylini also evolved from an ancestral stock not unlike the Alsodini and Grypiscini. The Grypiscini and Eleutherodactylini evolved direct development, which enabled these groups to invade regions lacking ponds. The evolution of these groups may have been prompted by avoidance of competition in the larval stage. The evolution of *Eleutherodactylus* is probably partly correlated with the Andean orogeny in the Mid-Tertiary. The Ceratophryinae and Odontophrynini represent groups that evolved in response to decreasing equability but were adapted to xeric, nonforested habitats. The principle low-equability adaptations of these groups involve a heavier, drier skin.

The Dendrobatidae are the low-equability adapted derivatives of the high-equability adapted Elosiinae. The similarities between the Dendrobatidae and Petropedetinae and the distributions of these two groups are suggestive of their evolution being synchronous with the last stage of separation of eastern Brasil and Africa. The Petropedetinae are low-equability adapted frogs. The radiation of the Dendrobatidae probably occurred during the Andean orogeny; the dispersal of the group into Central America is a Late Tertiary phenomenon (Savage, 1966). The Bufonidae may represent a paedomorphic offshoot of the Telmatobiinae rather than the Myobatrachinae. The heavy, frequently dermostosed skulls and thick, dry-adapted skin of bufonids suggest that this group evolved in response to decreasing equability. The antiquity of the group is not directly known, but the earliest fossils are Lower Miocene (North America and Europe). The most primitive genus is African (Tihen, 1960a), but the remainder of the genera are derived from the widespread *Bufo.* Among its derivatives are seven Neotropical, seven African, and five Malaysian and Philippine genera. *Bufo* ranges over all continents except Australia and Antarctica. The Bufonidae probably originated in Africa and South America when the two continents were connected. The early evolution and dispersal of the Bufonidae is considered syntopic with that of the Pipidae and characoid fishes. The Gymnophiona ex-

hibit a distribution and radiation pattern which is similar to that of the Bufonidae except that there is no caecilian genus which ranges over the Holarctic. The evidence suggesting that the Bufonidae represent an offshoot of the Myobatrachinae is meager. The mouthparts of the tadpoles of the two groups are similar. It is possible that the Bufonidae are a paedomorphic myobatrachine offshoot that invaded South America synchronously with the Telmatobiinae. If Antarctica was under a temperate regime of increasingly lower equability while Australia was under one of higher equability, it is conceivable that a low-equability adapted myobatrachine group evolved in Antarctica and dispersed into South America before the South America-Antarctica land bridge was obliterated in the Cretaceous. One serious objection to this hypothesis is the absence of any high-equability adapted bufonid genera in South America. *Rhinoderma* is a high-equability adapted genus and is related to the Bufonidae. Rhinodermatidae may represent this high-equability adapted proto-bufonid. The bufonid genus *Melanophryniscus* lives in areas of relatively high equability in northern Argentina and Uruguay but does not range southward into the zone of very high equability (58+). A further difficulty with the hypothesis is the requirement of a low-equability corridor through the high equability zone which presumably covered all of Patagonia during the Late Cretaceous and subsequent Tertiary. A more thorough study of *Rhinoderma* may prove to be the key in ascertaining the relationships of the Bufonidae to the Australo-Papuan or southern South American leptodactylids.

SUMMARY AND CONCLUSIONS

Based on the variation of behavorial and morphological characters, 57 Recent and three fossil genera of the Leptodactylidae are recognized. These 60 genera are placed in seven subfamilies, two of which are further subdivided into tribes. Two of the subfamilies (Cycloraninae and Myobatrachinae) occur only in the Australo-Papuan region, one (Heleophryninae) in southern Africa, and four (Ceratophryinae, Elosiinae, Leptodactylinae, and Telmatobiinae) in the Neotropical realm.[15]

The fossil record of leptodactylid frogs is of little value in deducing macrosystematic phylogeny. Fossils are represented in the Pleistocene of North America, the West Indies, and South America. Fossils of three phyletic lines are preserved in Lower Eocene to Pliocene deposits of Patagonia. All of the above-mentioned fossils are members of genera living in the same regions today or are closely related, extinct genera. The only zoogeographically important fossil is the Lower Eocene *Indobatrachus,* a myobatrachine from peninsular India. The subfamily Myobatrachinae is presently restricted to the Australo-Papuan region.

In order to determine the evolutionary direction (primitive to advanced) of several evolutionary trends, the following reasoning was used: character states shared by some or all archaic frog families and the other lissamphibian orders are primitive in the Anura; character states shared by most archaic frogs and most pelobatids are primitive in the Anura; and character states which are rare in the archaic families but always evident in the Pelobatidae are primitive in the pelobatid-bufonoid superfamily complex and may be primitive in all

[15] The alternatives to a single family arrangement are cited elsewhere (footnote 14, p. 204). The alternatives are: 1) two families, an Old World Myobatrachidae and a Neotropical Leptodactylidae; 2) two Old World families, an African-Australian group for the Cycloraninae and the Heleophryninae, an Australian group for the Myobatrachinae, and one Neotropical family; and 3) one Old World family and two Neotropical families, one for the two genera of the Ceratophryinae and a second for the other three Neotropical subfamilies. Other alternatives are simply permutations of the above.

frogs. This analysis resulted in the conclusion that the following character complexes are useful in ascertaining the relative primitiveness of frog groups: 1) type of cervical cotylar arrangement and type of occipital condylar arrangement; 2) neural arches—imbricate or not; 3) relative lengths of transverse processes of presacral vertebrae; 4) extent of dilation of sacral diapophyses; 5) presence of zygapophyses involved in sacral-coccygeal articulation; 6) separation of intervertebral discs from the centra; 7) complexity of the ilium; 8) loss of skull bones and teeth; 9) modifications of phalangeal formulae; 10) shape of pupil; 11) presence of outer metatarsal tubercles; 12) amplectic position; 13) egg size, oviposition site, larval development; 14) tadpole vent position; 15) tooth row formula of tadpole; and 16) architecture of pectoral girdle.

The Megophryinae (Pelobatidae) gave rise to four principle groups: 1) the Pelobatinae, 2) the Heleophryinae, 3) the Cycloraninae, and 4) the Myobatrachinae. Each of these groups appears to be an independent derivative. All of the Neotropical leptodactylids are probably descendants of one invasion of a cycloranine stock into South America. The Ceratophryinae and Telmatobiini are the most primitive Neotropical groups. The major leptodactylid radiation occurred within South America and radiated out of southern South America. One primitive tribe of the Telmatobiinae (Alsodini) gave rise to the advanced tribes of the subfamily (Grypiscini and Eleutherodactylini) as well as to two additional subfamilies (Elosiinae and Leptodactylinae). The Dendrobatidae are a derivative of the Elosiinae. The Telmatobiini and Odontophrynini are two tribes of the Telmatobiinae which appear to be the most primitive.

The evolution of leptodactylids is best explained on a superstructure involving continental drift. The following paleozoogeographic sequence is proposed: the basal stock, the Megophryinae, originated on northern landmasses from an ascaphid-discoglossid ancestor and dispersed southward in the Middle Mesozoic. A single dispersal corridor was utilized, the area in east Africa to the west of the East African Gulf of Tethys Sea. The megophryine stock could not invade South America because of the lack of a lowland corridor between North and South America or between Africa and the Brasilian shield. The stock passed through south Africa onto the southern landmass composed of peninsular India, Australia, and part of Antarctica. Progressive southerly extension of the East African Gulf isolated the derived group on India, Australia, and coastal Antarctica. During the Late Jurassic or early Cretaceous, a cycloranine stock dispersed along the coast of Antarctica into southern South America. Concurrently, climatic zonation and the ensuing decrease in climatic equability were bringing about the extinction of many groups of plants and animals. In the northern hemisphere, the Megophryinae gave rise to a low-equability adapted group, the Pelobatinae, and were restricted in distribution to a high-equability zone in southeast Asia. Lowering equability resulted in the isolation of the African megophryine derivative in the high-equability refugium in south Africa. This group is the Heleophryninae. The effect of decreasing equability in Australia was minor. The Cycloraninae evolved a low-equability tolerant group, the Limnodynastini. Decreasing equabilities with the northward movement of peninsular India during the Cretaceous and Tertiary resulted in the extinction of the myobatrachines living there. In South America, the more primitive leptodactylid genera survive in the area of high equability (often termed temperate South America). Decreasing equability resulted in the evolution of a low-equability adapted group, the Leptodactylinae. The Ceratophryinae and Odontophrynini are arid-adapted frogs and were therefore able to invade the low-equability areas which were arid or semi-arid.

Decreasing equabilities probably initially led to range restrictions which resulted in the isolation of the Elosiinae and Grypiscini in southeastern Brasil (a high-equability zone). The Dendrobatidae are low-equability adapted frogs which evolved from the high-equability adapted Elosiinae. The African ranids of the subfamily Petropedetinae are usually cited as ranids with adaptations paralleling the Neotropical dendrobatids. I have studied briefly the anatomy of *Petropedetes* and find the similarity to dendrobatids striking. The two family groups may represent remnants of a group once ranging across the South American-African isthmus. However, before the relationship can be established, more study of the ranids needs to be made.

In the course of this study, many taxonomic changes have been proposed. These are summarized below.

1. *Geobatrachus* Ruthven is removed from the Leptodactylidae and tentatively assigned to the Microhylidae, pending completion of a study of the systematic position of the genus by Dr. Charles F. Walker.

2. *Hylopsis platycephalus* Werner is a species of the Hylidae and perhaps not separable from *Hyla*.

3. *Rhinoderma* is placed in a monotypic family, the Rhinodermatidae.

4. The subfamily Cycloraninae is recognized for 10 genera. The subfamily is divided into two tribes: Cycloranini *(Cyclorana, Heleioporus, Neobatrachus,* and *Notaden)* and Limnodynastini new tribe *(Adelotus, Kyarranus, Lechriodus, Limnodynastes,* and *Philoria).*

5. The subfamily Myobatrachinae is recognized for one fossil and seven Recent genera *(Crinia, Glauertia, Indobatrachus, Metacrinia, Myobatrachus, Pseudophryne, Taudactylus,* and *Uperoleia).*

6. *Glauertia mjoebergi* is transferred to the genus *Uperoleia.*

7. *Taudactylus diurnus* is identical to *Crinia acutirostris;* the genus *Taudactylus* is worthy of recognition but the only species in the genus must now be called *T. acutirostris.*[16]

8. The subfamily Heleophryninae is recognized for the African leptodactylid, *Heleophryne.* The opinions of some earlier authors that *Heleophryne* is a ranid or the only genus of a monotypic ranoid family are rejected. The subfamily is similar to megophryine pelobatids but has achieved the leptodactylid grade.

9. The subfamily Ceratophryinae is recognized for two Recent genera *(Ceratophrys* and *Lepidobatrachus).* The group is not sufficiently different to be accorded family rank and is not more closely related to the Bufonidae than to other leptodactylids.

10. *Chacophrys* is considered a synonym of *Ceratophrys.*

11. *Stombus* Gravenhorst, 1825, is a synonym of *Ceratophrys* Wied, 1824; *Rana cornuta* Linné is designated the type-species of *Stombus.*

12. The Miocene fossil *Wawelia gerholdi* is a ceratophryine but is not separable from either *Ceratophrys* or *Lepidobatrachus* and is therefore tentatively recognized.

13. The subfamily Telmatobiinae is recognized for one fossil and 24 Recent genera of Neotropical leptodactylids. The following family group names are considered synonymous with the Telmatobiinae: Hylodidae Günther, 1859, Alsodina Mivart, 1869, Cacotina Mivart, 1869, Grypiscina Mivart, 1869, Cyclorhamphinae Lutz, 1954, Eleutherodactylinae Lutz, 1954, Calyptocephalellinae Reig, 1960, and Batrachylinae Gallardo, 1965. The subfamily is divided into five tribes: Telmatobiini *(Batrachophrynus, Caudiverbera, Neoprocoela, Telmatobius,* and *Telmatobufo),* Alsodini *(Batrachyla, Eupsophus, Hylorina,* and *Thoropa),* Odontophrynini new tribe *(Odontophrynus* and *Proceratophrys),* Grypiscini *(Crossodactylodes, Cycloramphus,* and

[16] M. J. Tyler *(in litt.)* informed me that this statement is erroneous. The two species of *Taudactylus* are distinctive species. The materials used in this work are *T. acutirostris* (Andersson).

Zachaenus), and Eleutherodactylini (*Amblyphrynus, Eleutherodactylus, Euparkerella, Holoaden, Hylactophryne, Ischnocnema, Niceforonia, Sminthillus, Syrrhophus,* and *Tomodactylus*). A new genus, *Scythrophrys*, is named for *Zachaenus sawayae* Cochran but cannot be confidently assigned to a tribe until osteological data are available.

14. The generic name *Caudiverbera* is used in preference to *Calyptocephalella*. *Eophractus* Schaeffer is placed in the synonymy of *Caudiverbera*. *Gigantobatrachus parodii* (Miocene of Patagonia) and *Calyptocephalella canqueli* (Oligocene of Patagonia) are placed in the synonymy of *Caudiverbera caudiverbera*.

15. *Neoprocoela* is not a synonym of *Bufo* and is recognized as a genus of leptodactylid frogs which is ancestral to *Batrachophrynus*.

16. *Telmatobufo* is not a synonym of *Aruncus; Aruncus* is a synonym of *Bufo*.

17. *Macrogenioglottus* is placed in the synonymy of *Odontophrynus*.

18. *Proceratophrys* is the valid generic name for the supraspecific group frequently called *Stombus*.

19. *Craspedoglossa* is considered a synonym of *Zachaenus*.

20. *Zachaenus roseus* Cope is not a member of the genus *Zachaenus* and is considered a *species inquirenda* in the Leptodactylidae, probably in the Telmatobiinae.

21. *Noblella* is placed in the synonymy of *Eleutherodactylus*.

22. *Pseudohyla*, previously considered a hylid genus or a synonym of *Hyla*, is a synonym of *Eleutherodactylus*.

23. *Eupsophus wettsteini* is transferred to the genus *Niceforonia*.

24. *Syrrhophus laplacai* is probably a member of the genus *Niceforonia*.

25. *Syrrhophus* is not a synonym of *Eleutherodactylus*, but the separation of *Syrrhophus* and *Tomodactylus* is considered tenuous.

26. The subfamily Elosiinae is recognized for three Recent genera (*Crossodactylus, Hylodes,* and *Megaelosia*). *Hylodes* Fitzinger is used in preference to *Elosia* Tschudi.

27. The subfamily Leptodactylinae is recognized for ten Neotropical genera (*Barycholos, Edalorhina, Hydrolaetare, Leptodactylus, Limnomedusa, Lithodytes, Paratelmatobius, Physalaemus, Pleurodema,* and *Pseudopaludicola*).

28. *Paratelmatobius pictiventris* A. Lutz, *in* Lutz and Carvalho, is a *nomen nudum* and an obligate synonym of *Paratelmatobius gaigeae* (Cochran).

29. *Pseudopaludicola boliviana* Parker is considered a synonym of *P. pusilla* (Ruthven).

30. *Leptodactylus abavus* Holman (Lower Miocene of Florida) is a *Rana* and questionably separable from *Rana miocenica* Holman of the same horizon and locality.

31. *Eorubeta nevadensis* Hecht (Lower Eocene of Nevada) is not a leptodactylid and is considered "Family *incertae sedis*, Order Salientia."

32. The following new taxa are proposed: Limnodynastini new tribe, Odontophrynini new tribe, and *Scythrophrys* new genus (type-species *Zachaenus sawayae* Cochran, 1953).

APPENDIX

The following is an alphabetical list of the species and specimens used in formulating the generic accounts for the Leptodactylidae. In addition to the museum abbreviations listed on page 17, the following abbreviations (and the name of the institution) are used below:

CAS	California Academy of Science
LHUBA	Laboratorio Herpetologica Universidad Buenos Aires
NMW	Naturhistorisches Museum Wien
WAM	Western Australia Museum

Unless otherwise noted, the specimens listed below are dry skeletons. Specimens which were cleared and stained are indicated by "CS"; those which were studied with stereoradiographs are indicated by "SRG."

Adelotus brevis.—AMNH 59489-90, KU 56242.

Amblyphrynus ingeri.—FMNH 54591 (SRG).

Barycholos pulcher.—UMMZ S-2881 (CS).

Batrachophrynus macrostomus.—KU 98127-28.

Batrachyla leptopus.—UMMZ S-2246 (CS).

Batrachyla taeniata.—UMMZ S-2247 (CS).

Caudiverbera caudiverbera.—AMNH 23622, 23958, 24016, 51510, FMNH 9703.

Ceratophrys aurita.—EHT 1415, FMNH 51703-04, KU 98129.

Ceratophrys calcarata.—KU 69844, JDL S-76, 237-40, 1189.

Ceratophrys ornata.—UMMZ 98834 (tadpole, CS), 109753 (juvenile, CS).

Crinia signifera.—AMNH 40291, KU 56243-49 (CS), 56364 (CS).

Crossodactylodes pintoi.—USNM 102611 (CS).

Crossodactylus dispar.—KU 92753 (CS).

Crossodactylus gaudichaudi.—KU 92759 (CS), JDL S-265, 283-84, 417-19.

Crossodactylus grandis.—KU 92765 (CS).

Cycloramphus asper.—KU 92773.

Cycloramphus dubius.—KU 92780.

Cycloramphus eleutherodactylus.—KU 92785.

Cycloramphus fulginosus.—KU 92790-91.

Cycloramphus granulosus.—KU 92795 (CS).

Cycloramphus ohausi.—KU 92801 (CS).

Cycloramphus pinderi.—KU 92807.

Cyclorana australis.—AMNH 62228, KU 93549 (CS), 93550.

Cyclorana cultripes.—AMNH 67232 (CS), KU 110324.

Cyclorana dahli.—UMMZ 65250.

Cyclorana platycephalus.—KU 110329.

Edalorhina perezi—AMNH 52847, KU 124225 (CS), 124226.

Eleutherodactylus abbotti.—AS X1795 (CS), X2006 (CS).

Eleutherodactylus achatinus.—KU 119472 (CS).

Eleutherodactylus antillensis.—AS 12083 (CS), 12104 (CS).

Eleutherodactylus areolatus.—KU 118129 (CS), 119501 (CS).

Eleutherodactylus armstrongi.—KU 110347 (CS), JDL S-236.

Eleutherodactylus atkinsi.—AS V6263 (CS).

Eleutherodactylus audanti.—JDL S-235.

Eleutherodactylus auriculatoides.—AS X-9200 (CS).

Eleutherodactylus barlagnei.—MCZ 35331.

Eleutherodactylus binotatus.—KU 92813 (CS).

Eleutherodactylus biporcatus.—KU 41047, 105903.

Eleutherodactylus bogotensis.—KU 110408-09 (CS).

Eleutherodactylus bransfordi.—KU 25217, 41032, 103036-41 (CS), JDL S-243, 401.

Eleutherodactylus brederi.—KU 77670 (CS).

Eleutherodactylus brevicrus.—KU 108982 (CS).

Eleutherodactylus bufoniformis.—KU 80621.

Eleutherodactylus caryophyllaceus.—KU 68261 (CS).

Eleutherodactylus cerasinus.—KU 103026-27 (CS).

Eleutherodactylus chloronotus.—KU 118130-33 (CS), JDL S-247, 260, 335.

Eleutherodactylus cochranae.—AS V8014 (CS).

Eleutherodactylus conspicillatus.—KU 108988 (CS).

Eleutherodactylus coqui.—KU 79924 (CS), 79947-50 (CS).

Eleutherodactylus crassidigitatus.—KU 68262 (CS).

Eleutherodactylus croceoinguinis.—KU 109086 (CS).

Eleutherodactylus cruentus.—KU 102998 (CS), 107941-42 (CS), 117353-54.

Eleutherodactylus cundalli.—AS 15128 (CS), 15711 (CS).

Eleutherodactylus curtipes.—KU 109052-58 (CS), JDL S-252-54, 261, 310, 337-38, 342-43, 351, 402, 430-31.

Eleutherodactylus devillei.—UIMNH 55833 (CS).

Eleutherodactylus diastema.—KU 41033-35, 68263 (CS), 80636 (CS), JDL S-244, 441.

Eleutherodactylus eneidae.—AS 12637 (CS), 12758 (CS).

Eleutherodactylus engytympanum.—KU 102999-3007 (CS), 117355-57.

Eleutherodactylus fitzingeri.—KU 77658, 117358-62, JDL S-407-08.

Eleutherodactylus fleischmanni.—KU 65790 (CS), 68157-58, 68264-65 (CS).

Eleutherodactylus florulentus.—KU 102242-46 (CS).

Eleutherodactylus frater.—KU 80637 (CS).

Eleutherodactylus furcyensis.—AS X2018 (CS).

Eleutherodactylus gaigeae.—KU 106297-98 (CS).

Eleutherodactylus galdi.—USNM GOV 8944 (CS).

Eleutherodactylus gollmeri.—KU 41036-37.

Eleutherodactylus gossei.—AS 13795 (CS), 14464 (CS), 15677 (CS).

Eleutherodactylus guentheri.—KU 92819 (CS).

Eleutherodactylus haitianus.—AS X8296 (CS).

Eleutherodactylus inoptatus.—AS X2356.

Eleutherodactylus jugans.—MCZ 19856 (2) (CS).

Eleutherodactylus karlschmidti.—AS 12760 (CS).

Eleutherodactylus lentus.—AS V7395 (CS).

Eleutherodactylus locustus.—AS 11867 (CS), 11881 (CS).

Eleutherodactylus longirostris.—KU 77671 (CS).

Eleutherodactylus macdougalli.—UIMNH 40941 (CS).

Eleutherodactylus martinicensis.—MCZ 35321.

Eleutherodactylus melanostictus.—KU 107943 (CS).

Eleutherodactylus mexicanus.—KU 55592-95 (CS), 55596-98, 55599-600 (CS), 55622, 103008-15 (CS), JDL S-1261-62.

Eleutherodactylus minutus.—AS X8939 (CS).

Eleutherodactylus molinoi.—KU 80635 (CS).

Eleutherodactylus montanus.—AS X8313 (CS), X8479 (CS).

Eleutherodactylus nasutus.—KU 92822 (CS).

Eleutherodactylus nigriventris.—KU 92739 (CS).

Eleutherodactylus nigrovittatus.—USNM GOV 8108 (CS).

Eleutherodactylus nubicola.—AS 12891 (CS), 12898 (CS).

Eleutherodactylus occidentalis.—KU 102598 (CS), 104101 (CS).

Eleutherodactylus octavioi.—KU 92828 (CS).

Eleutherodactylus orcutti.—AS 13373 (CS).

Eleutherodactylus ornatissimus.—KU 119749 (CS).

Eleutherodactylus palmatus.—KU 41038.

Eleutherodactylus palmeri.—KU 110913 (CS), 110923 (CS), JDL S-242, 397.

Eleutherodactylus pantoni.—AS 13494 (CS), 13747 (CS).

Eleutherodactylus parvus.—KU 92834 (CS).

Eleutherodactylus patriciae.—KU 79770-71 (CS), 79794 (CS).

Eleutherodactylus peruvianus.—(paratype of *Sminthillus peruvianus*) AMNH not catalogued (CS).

Eleutherodactylus pictissimus.—AS X2750 (CS), X2813 (CS).

Eleutherodactylus planirostris.—KU 92656 (CS), JDL S-230, 245, 1068.

Eleutherodactylus podociferus.—KU 41049, 68266 (CS), 80644 (CS), 103017-24 (CS).

Eleutherodactylus portoricensis.—AS 11710 (CS).

Eleutherodactylus punctariolus.—KU 117363.

Eleutherodactylus pygmaeus.—KU 103025 (CS), JDL S-15, 25, 1311, UIMNH 15141 (CS), 16132 (CS), 40335 (CS), 49268 (CS), 49275 (CS).

Eleutherodactylus rhodopis.—UIMNH 14729 (CS), 47996 (CS), 49192 (CS), 49194 (CS), 49211 (CS).

Eleutherodactylus richmondi.—AS 12623 (CS).

Eleutherodactylus ricordi.—AMNH 63439 (CS), 63450 (CS).

Eleutherodactylus ridens.—KU 102996-97 (CS).

Eleutherodactylus rugulosus.—KU 59877-79, 84891, JDL S-17, 67, 1006, 1238-51, UIMNH 14756 (CS).

Eleutherodactylus ruthae.—AS V4237 (CS).

Eleutherodactylus spatulatus.—KU 87781 (CS).

Eleutherodactylus sulcatus.—KU 100355, 124227 (CS).

Eleutherodactylus surdus.—JDL S-268, 357-58, 360.

Eleutherodactylus talamancae.—KU 68267-68 (CS), 117364.

Eleutherodactylus trepidotus.—KU 118134-35 (CS), UIMNH 55874 (CS).

Eleutherodactylus unistrigatus.—KU 111136-37 (CS), JDL S-263, 269, 332, 340, 392-95, 530-31.

Eleutherodactylus variabilis.—KU 109094 (CS).

Eleutherodactylus venancioi.—KU 92839 (CS).

Eleutherodactylus weinlandi.—AS V1718 (CS), V2466 (CS).

Eleutherodactylus whymperi.—JDL S-248-51, 270, 446.

Eleutherodactylus wightmanae.—AS 12704 (CS), 12739 (CS).

Eleutherodactylus w-nigrum.—KU 119857 (CS).

Eleutherodactylus zugi.—AMNH 63269-70 (CS).
Euparkerella brasiliensis.—KU 93192 (CS).
Eupsophus juninensis.—MCZ 24360 (CS).
Eupsophus roseus.—AMNH 22104, KU 84731 (CS).
Glauertia russelli.—WAM R22920 (CS).
Heleioporus albopunctatus.—UMMZ not catalogued.
Heleioporus australiacus.—AMNH 59491.
Heleioporus eyeri.—UMMZ 124504.
Heleophryne natalensis.—KU 105925 (CS).
Holoaden bradei.—KU 92868 (CS), 107087-88 (CS).
Hydrolaetare schmidti.—KU 110613.
Hylactophryne augusti.—KU 56187, 56192 (CS), UMMZ S-2695.
Hylodes aspera.—KU 92870 (CS), 92875.
Hylodes lateristrigata.—KU 92878 (CS).
Hylodes magalhaesi.—KU 92887 (CS).
Hylodes nasus.—KU 74209 (CS), 92893-94, JDL S-255-56, 258, 282.
Hylodes pulcher.—KU 92899 (CS), 92900.
Hylorina sylvatica.—BMNH 91.29.17, FMNH 7102 (SRG), 7107 (SRG).
Ischnocnema quixensis.—KU 104388, UIMNH 59643 (CS).
Kyarranus sphagnicola.—AMNH 64294, KU 110331 (CS).
Lechriodus fletcheri.—AMNH 59488, CAS 82221 (CS).
Lepidobatrachus asper.—KU 80783.
Leptodactylus albilabris.—UMMZ S-166.
Leptodactylus bolivianus.—KU 41026.
Leptodactylus bufonius.—KU 92905.
Leptodactylus chaquensis.—KU 80795.
Leptodactylus gracilis.—KU 92913-14.
Leptodactylus hylaedactylus.—KU 119387-88 (CS).
Leptodactylus labialis.—KU 41027, 68273-74 (CS).
Leptodactylus macrosternus.—KU 92919-20.
Leptodactylus melanonotus.—KU 68275-76 (CS), JDL S- 1252-58, UMMZ S-858, 1045.
Leptodactylus mystaceus.—KU 92932.
Leptodactylus mystacinus.—KU 92925-26.
Leptodactylus pentadactylus.—KU 41028-29, 68159, 84981-82, 117366-68.
Leptodactylus podicipinus.—KU 92938.
Leptodactylus prognathus.—KU 80824 (CS), 92944.
Leptodactylus pustulosus.—KU 92947.
Leptodactylus quadrivittatus.—KU 41030.
Leptodactylus syphax.—KU 92951.
Leptodactylus wagneri.—KU 104389-90.
Limnodynastes dorsalis.—KU 93553, UMMZ S-165.
Limnodynastes fletcheri.—KU 93559 (CS).
Limnodynastes peronii.—KU 93566 (CS).
Limnodynastes tasmanensis.—AMNH 60589, KU 93573-74 (CS).
Limnomedusa macroglossa.—KU 92960 (CS), 92961.
Lithodytes lineatus.—KU 104340 (CS).
Megaelosia goeldi.—KU 92965-66, 106271.
Metacrinia nichollsi.—KU 110332 (CS).
Mixophyes fasciolatus.—KU 56627.
Myobatrachus gouldii.—KU 110333 (CS).
Neobatrachus centralis.—KU 93578.
Neobatrachus pictus.—FMNH 97281, KU 69278 (CS).
Niceforonia festae.—KU 118137 (CS), USNM 160944 (CS), 160950 (CS).
Niceforonia flavomaculata.—KU 119743 (CS).
Niceforonia montia.—MCZ 24352 (CS).
Niceforonia wettsteini (paratypes of *Eupsophus wettsteini*).—NMW 15846:1-2 (SRG).
Notaden bennetti.—FMNH 97658.
Notaden nichollsi.—KU 93580 (CS), 93582 (CS).
Odontophrynus americanus.—KU 92968, 100437.
Odontophrynus carvalhoi.—KU 100441-42.
Odontophrynus cultripes.—KU 92975.
Odontophrynus occidentalis.—LHUBA 1200, 1218.
Paratelmatobius lutzi.—KU 92981 (CS), 107089 (CS).
Philoria frosti.—KU 50699 (CS).
Physalaemus albonotatus.—KU 92987 (CS).
Physalaemus biligonigerus.—KU 84768-76.
Physalaemus centralis.—KU 92993 (CS).
Physalaemus cuvieri.—KU 92999 (CS).
Physalaemus ephippifer.—KU 93005 (CS).
Physalaemus fuscomaculatus.—KU 80811 (CS), 93010 (CS), UMMZ S-2357 (CS).
Physalaemus gracilis.—KU 93016 (CS).
Physalaemus maculiventris.—KU 93022 (CS).
Physalaemus nanus.—KU 93025 (CS).
Physalaemus nattereri.—KU 92844 (CS), 92845.
Physalaemus petersi.—KU 120290 (CS).
Physalaemus pustulatus.—KU 118136 (CS).
Physalaemus pustulosus.—KU 41031, 68269-72 (CS), JDL S-1204.
Physalaemus signiferus.—KU 93033 (CS).
Pleurodema bibroni.—FMNH 3746-47, 3758.
Pleurodema brachyops.—AMNH 69754, KU 96159, 104318 (CS), UIMNH WLB-725 (CS).
Pleurodema cinerea.—KU 80836, 93038.
Pleurodema diplolistris.—KU 93044 (CS), UMMZ 108521 (CS), 108895 (6) (CS).
Proceratophrys appendiculata.—KU 93070.
Proceratophrys boiei.—KU 93076.
Proceratophrys cristiceps.—KU 106273, UMMZ 115658.
Pseudopaludicola ameghini.—KU 93050 (CS).
Pseudopaludicola falcipes.—KU 93056 (CS).
Pseudopaludicola pusilla.—UMMZ 54589(2) (CS); *boliviana topotypes,* UMMZ (2), not catalogued (CS).
Pseudopaludicola saltica.—KU 93068 (CS).
Pseudophryne bibroni.—KU 93588 (CS).

Pseudophryne corroboree.—AMNH 64510-12.

Scythrophrys sawayae.—USNM 125530 (holotype), not a skeletal preparation; some skeletal features were observed through slits in the skin.

Sminthillus limbatus.—KU 68684 (CS).

Syrrhophus guttilatus.—JDL S-1215.

Syrrhophus leprus—JDL S-992, UIMNH 27130 (CS).

Syrrhophus marnockii.—JDL S-214.

Syrrhophus pallidus.—KU 80320 (CS).

Syrrhophus pipilans.—KU 59950 (CS).

Syrrhophus rubrimaculatus.—UIMNH 55313-16 (CS).

Taudactylus acutirostris.—KU 124233 (CS).

Telmatobius hauthali.—KU 72879 (CS), UMMZ S-164.

Telmatobius marmoratus.—UMMZ 68179 (2).

Telmatobius patagonicus.—KU 80781 (CS).

Telmatobufo bullocki.—FMNH 23842 (SRG).

Thoropa lutzi.—KU 92850 (CS), 92908 (CS).

Thoropa miliaris.—KU 92855 (CS), 92856.

Thoropa petropolitana.—KU 92862 (CS).

Tomodactylus albolabris.—KU 87780 (CS).

Tomodactylus grandis.—UMMZ S-963.

Tomodactylus nitidus.—KU 102649 (CS), JDL S-1308, UIMNH 7830 (CS), 7832-34 (CS), UMMZ S-2225.

Uperoleia rugosa.—AMNH 13336, KU 109861 (CS).

Zachaenus parvulus.—KU 93082 (CS), 107090 (CS), 107091.

Zachaenus roseus.—USNM 15126 (holotype).

Zachaenus stejnegeri.—KU 92742 (CS), 92747.

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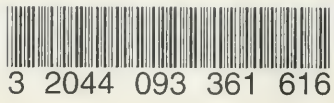
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